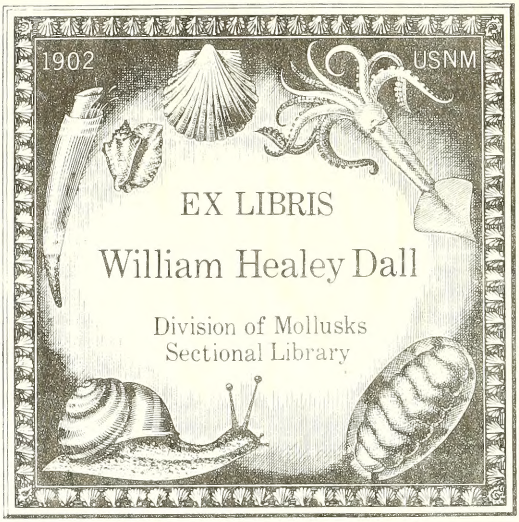

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CONTRIBUTION TO THE NATURAL HISTORY OF THE PEARLY NAUTILUS.

BY ARTHUR WILLEY, D.SC. LOND., HON. M.A. CANTAB.
Director of the Colombo Museum, Ceylon.

I. PERSONAL NARRATIVE.

With 18 Text-figures.

II. SPECIAL CONTRIBUTION.

With Plates LXXV.—LXXXIII., a Map, and 15 Text-figures.

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By ARTHUR WILLEY, D.Sc., F.R.S.

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ERRATA.

1. "Blanche River" where it occurs should read "Blanche Bay."

2. In the article by the late Mr Bedford on Holothurians the word "topotype" was wrongly employed at my instigation. It should read "local variety."

[Reprinted from *A. Willey's Zoological Results. Part VI.*
Cambridge University Press. *May*, 1902.]

CONTRIBUTION TO THE NATURAL HISTORY OF THE PEARLY NAUTILUS.

BY ARTHUR WILLEY, D.SC. LOND., HON. M.A. CANTAB.
Director of the Colombo Museum, Ceylon.

I. PERSONAL NARRATIVE.

With 18 Text-figures.

LONGUM PER MARE, SED FAVENTIS UNDAE.

As I have already explained in the prefatory note which accompanied the first Part of these Zoological Results, my journey to the Eastern Archipelago was promoted by the Managers of the Balfour Studentship in the University of Cambridge, with the avowed object of procuring material for the study of the embryonic development of the pearly Nautilus. It is well known that this molluscan type occupies a comparatively isolated position in the series of existing animal forms, and that it is a surviving relic of an order which was dominant in former geological epochs. It is in fact one of the best examples of what have been called persistent types or, by way of paradox, living fossils, that is to say, relict types of pre-tertiary creation.

It has been an object of serious investigation on the part of many of the foremost zoologists of England, France, Germany and Holland during the nineteenth century, and it was even one of Cuvier's regrets that he had never seen the inhabitant of the chambered shell which had been, from time immemorial, an ornament of the conchologist's cabinet.

Of course the chance of acquiring a complete set of developmental stages of such a type as this, from the moment of deposition of the eggs, through the period of incubation, culminating finally in the hatching of the miniature organism, would be enough to whet the enthusiasm and claim the devotion of any zoologist. The distinguished German naturalist, Dr Richard Semon, whose journey to Australia, "the land of living fossils," has resulted not only in the publication of an imposing array of technical monographs, but also in the composition of a delightfully instructive book, spent some time at Amboyna, and tells us that a principal aim of his stay on the Moluccas was the study of Nautilus's development[1]. Elated by his successes in Australia, Semon began to imagine himself "the happy possessor of a perfect series of developing *Nautilus pompilius.*" In this, however, he was disappointed, and it will be seen that my efforts were only crowned by partial success, an eventuality for which I had prepared my mind beforehand.

---

[1] Semon, R., *In the Australian Bush*, 1899, pp. 423 and 486.

A locality where *Nautilus* apparently abounded had been made known, directly or indirectly, through the instrumentality of the Wesleyan Mission in New Britain, now known as Neu-Pommern, an island of the Bismarck Archipelago which forms part of the German possessions in Papua.

Thither I resorted in the autumn of 1894, generously supported by many letters and introductions from Professor E. Ray Lankester, Professor A. A. W. Hubrecht, Sir William Flower, Dr Anton Dohrn, the Rev. G. W. Olver of the Wesleyan Missionary Society, Rev. W. H. Dallinger, and the authorities of the Foreign Office in Berlin and of the German New Guinea Company.

On the way to Singapore I took occasion to call at the Stazione Zoologica at Naples, where I had previously occupied the table of the British Association. Dr Dohrn very kindly offered to give me an introduction to a gentleman, whose book I had just been reading[1], but of whose present whereabouts I had no information. This was Mr Richard Parkinson of Ralum, New Britain, whose name is well known to ethnographers, and whose house is a refuge for wayfaring strangers in those parts. The hospitality shown to me by Mr and Mrs Parkinson, and their family, on my arrival and during my sojourn in New Britain, was something of which I had not dreamt at the outset of my journey, and their acquaintance with the natives, resulting from long residence in the country, together with their readiness to do all in their power to help forward my work, enabled me to commence operations without delay.

As the ship approached the anchorage opposite Herbertshöhe (Kokopo) and I obtained my first near view of the Gazelle Peninsula of New Britain, the rising coast with its variegated sky-line, groves of waving cocoa-nut palms, scattered homesteads, with the slumbering volcanic sentinels (the Mother and Daughters) to the right, presented a fascinating prospect.

One of my first cares, after the first blush of arrival was over, was to procure a boat, and this was quickly arranged by the good offices of Mr Parkinson and the obliging kindness of the Rev. Père Helfer, acting chief of the Catholic Mission at Kininigunan, during the temporary absence of the Bishop, Monsignor Coupé. At this time of the year (the middle of December) the north-west monsoon prevails, and dangerous squalls of startling suddenness and severity are of frequent occurrence. Two days later the worthy Father Helfer met his doom through the swamping of a boat, in which he was proceeding to the island of Matupi in Blanche Bay, to procure decorations for the Christmas festivities at the Mission.

For a long time I placed much reliance upon the services of a man named To-mangiau, who was, indeed, something of a rascal, a *diable boiteux*, one leg being shorter than the other, but not without his points and a good swimmer. Shortly after I made his acquaintance he let himself be tattooed with a broken beer-bottle:—two concentric circles over each breast blackened with burnt cocoa-nut. I have also seen the natives using chips of glass and fragments of obsidian as lancets for blood-letting.

---

[1] Parkinson, R., *Im Bismarck-Archipelago*, Leipzig, 1887. If I remember rightly, I owed my knowledge of the existence of this interesting work to Dr Otto Finsch, whom I consulted at Delmenhorst before leaving Europe.

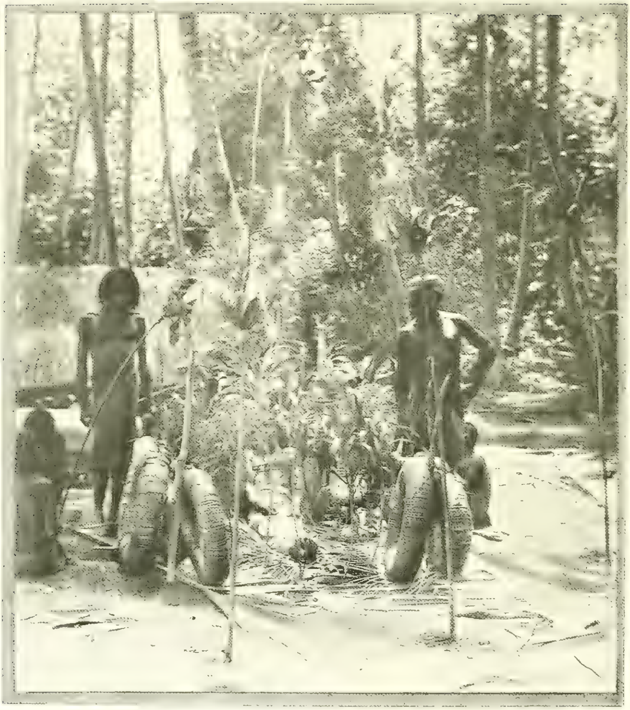

Fig. 1. Exhibition of coils of diwara at the obsequies of a native (To-nonat) of the Gazelle Peninsula.

To face page 693

This practice of bleeding at the seat of pain is resorted to in cases of headache, abdominal and muscular pains.

On Christmas Eve (1894) some natives brought a white, freshly limed canoe to Ralum for sale, the price being twenty fathoms of native shell-money or diwara[1], approximately equivalent to forty shillings. As I did not possess a shell in the world I was unable to conclude the bargain, much as I desired it. The shells (*Nassa callosa*, var. *camelus*) are obtained by barter and by collecting from a distant locality on the north coast of New Britain, and the bleaching, perforating[2] and threading upon rattan slips, involve so much time and labour, only good shells of even size being accepted, that the diwara is regarded as sacred or "tambu" and is relatively as difficult to acquire in that country as gold is in Europe. By attending a funeral on one occasion and demanding compensation for a stolen fish-basket on another, I came into a little property, but nothing worthy of mention.

Much formality attends transactions in which "diwara" changes hands, the most important being, of course, the purchase of a wife. The rich hoard up their wealth in "tambu" houses, in the form of huge coils containing many hundred fathoms of the rattan fibre with the shells threaded upon it, each coil being wrapped up in dried banana leaves and, in this condition, resembling a life-belt. These coils are rarely broached during a man's lifetime but, at his death, they are opened and divided into lengths varying from less than a fathom to several fathoms, which are distributed with singular liberality amongst those who assist at the obsequies.

The principal scene of my operations in the search for *Nautilus* in New Britain was situated in Blanche Bay, a deep inlet at the north-eastern end of the Gazelle Peninsula, which has received the picturesque native name "a bit na ta," the source of the sea; and, indeed, it needs but little imagination, more especially in squally weather, when clouds are gathering over the mountain-tops, to admit the poetic justice of this ambitious appellation.

I commenced by purchasing a loosely built, palm-thatched hut on the island of Rakaiya or Raluan[3], from a man called To-vungia[4], chief of the village of Davaun, to whom I was introduced by Mrs Parkinson, whose knowledge of the language and usages of these natives is very thorough. The price paid for the hut was one hundred sticks of trade tobacco. The island itself is uninhabited, the greater part of it having been elevated above sea-level as the result of a volcanic disturbance in the year 1878. A small volcano, also called Rakaiya, *i.e.* the spirit, occurs at the base of the South Daughter and is still simmering, sometimes emitting flames. The great drawback to a residence on the island lies in the fact that there is no freshwater source on it. It is now largely covered with *Casuarina* trees, and near one end there is a dark lagoon-like enclosure which is separated from the sea at low tide.

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[1] Sometimes written "dewarra." Cf. Dr O. Finsch, *Ethnologische Erfahrungen aus der Südsee*, Wien, 1893, p. 387.

[2] The shells are converted into beads by dexterously knocking off the curious hump, an operation which is performed by women.

[3] Also called Vulcan Island.

[4] All men's names in this district begin with the prefix "To-"; names of women begin with "Ya-."

My hut was quite open on the lee-side, and there were rents in the thatching which gaped wider when my boatmen abstracted handfuls of the desiccated leaflets for the purpose of lighting the fire. Of course I put a stop to this practice as soon as I detected it, and my folding bedstead and mosquito curtain, with other impedimenta, made the place habitable for about a month, after which I moved into more commodious quarters afforded by a Chinese trader's house at Karavia, a village lying opposite to Raluan on the mainland.

During my tenure of the hut on Raluan, To-vungia honoured me with several visits, generally accompanied by a crowd of retainers who clustered round the threshold of my primitive abode, no doubt thinking that my occupation was only worthy of a white man. When I first knew To-vungia he was unregenerate and interesting, with the long cord-like, half-bleached, tawny, pendent, spiral locks which are characteristic of these natives and also of some of the Solomon Islanders[1].

These visits were not always a source of unmixed pleasure, their inquisitive disposition leading some of the visitors to investigate the penetralia of my hut with scant ceremony and somewhat to my disgust when, as too often happened, they were afflicted with appalling sores.

Meanwhile as I had a great quantity of baggage to store away, including dredges, laboratory appliances and other more or less necessary encumbrances, Mr Parkinson kindly detailed some of the native labourers on the plantations, to erect a rain-proof shelter of bamboos and plaited palm-leaves on the beach in the Ralum district at a spot called Ka-ra-koai, meaning "under the mango-trees," of which there were three in the vicinity. No flooring was laid down, as the black tufaceous soil is so porous that the heaviest downpour of rain sinks immediately below the surface. Care had to be taken not to place wooden cases on the bare earth on account of the ravages of the white ants (termites) to which they would be exposed. Small cylinders of bamboo (which is proof against termites) laid upon the ground under the cases, afforded sufficient protection for the time being, and I stored various articles in this place and even worked here occasionally, although it was not possible to bring fresh material from Blanche Bay, the distance being too great.

As I was quite ignorant of the mode of propagation of *Nautilus*, I employed all available methods in my preliminary researches with the idea of arriving at my object by a process of exclusion. These methods included the investigation of the superficial waters of the bay by means of the tow-net, in order to determine the nature of the Plankton or drift-fauna (Auftrieb) of this locality, since many animals which live close in-shore or at the bottom in moderate depths (less than a hundred fathoms), lead a roving pelagic life during the early stages of their development.

Besides pelagic larvae of Mollusca, Annelida, Echinoderma and Anthozoa, the invertebrate Plankton also includes many adult animals which affect a pelagic environment throughout life. These are distinguished by the excessive transparency of their tissues, which renders necessary a careful blending of the light before their structure

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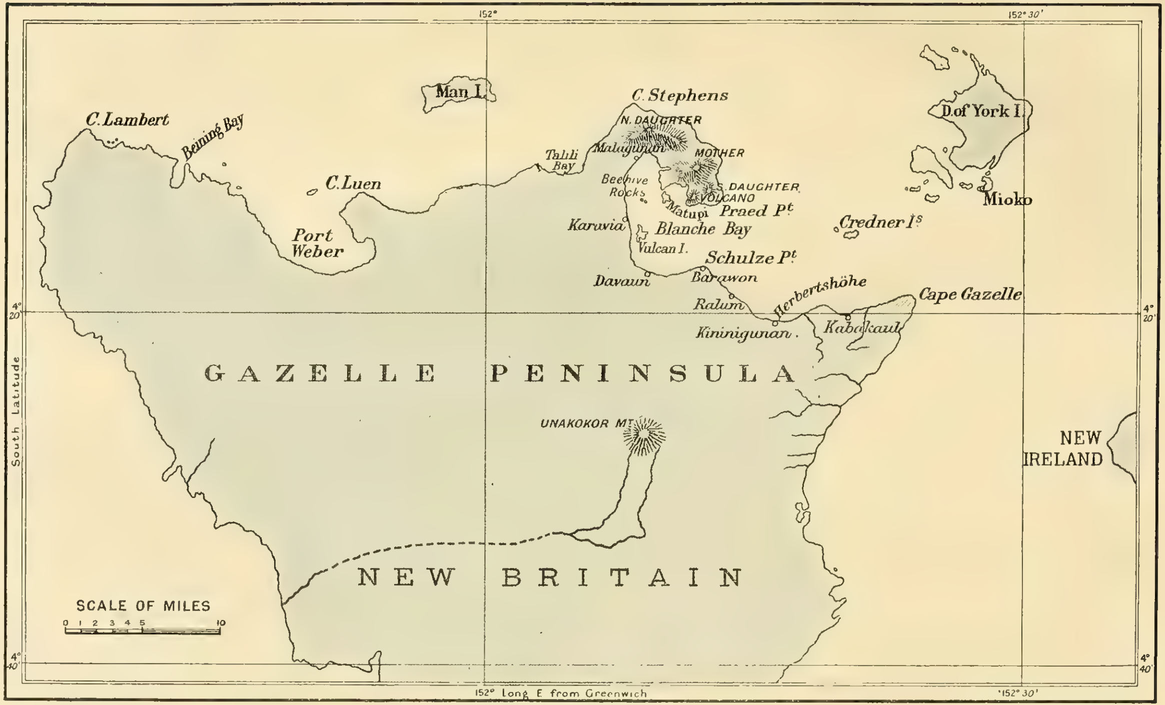
[1] Admirable photographs of the New Britain natives taken by Mr Parkinson have been published in the *Album der Papúa-Typen*, edited by A. B. Meyer and R. Parkinson, Dresden, 1894.



London Stanford's Geog¹ Estab^t.

FIG. 2. Map of the Gazelle Peninsula.

can be made out under a microscope or simple lens. I have given sketches of the *Tornaria* (larva of Enteropneusta), which I obtained in the New Britain Plankton in Part III. (p. 286) of this publication. Among many other objects, a small pelagic Mollusc known as *Atlanta*, belonging to the sub-order Heteropoda, was abundant at various depths. It was my first acquaintance with this small creature which is almost absurdly like a miniature *Nautilus*. It possesses in fact a perfect involute planorbiform shell, laterally compressed, symmetrical on both sides[1] and not exceeding 5 millimetres in major diameter. Of course it differs essentially from *Nautilus* in that the cavity of the shell is not divided into chambers and the orifice is directed downwards, *i.e.*, towards the back of the animal.

Another frequent component of the Plankton consisted of the *Appendiculariae*, small pelagic Ascidians which permanently retain a caudal appendage only present during the larval phase in the life-history of the fixed Tunicata. I was somewhat surprised to find specimens of a bright yellow colour and others brilliant blue, not knowing previously that these pellucid animals ever possessed any pigmentation. It has, however, recently been noted by Mr E. T. Browne that specimens of the genus *Oikopleura* occurring in British waters are sometimes coloured a bright crimson[2].

More important than these Plankton excursions, which generally took place in the small hours of the morning before sunrise, was the investigation of the nature of the ground at the bottom of the sea in Blanche Bay. This revealed the existence of submarine chasms probably inaccessible to the dredge, and it may be at once noted as a possibility that such protected situations are naturally chosen by *Nautilus* for the purposes of nidification and oviposition.

In order to clinch matters at the outset I seized the opportunity of engaging, by favour of Herr Thiel, the representative of the firm of Messrs Hernsheim and Company on the island of Matupi in Blanche Bay, the services of a small steam-launch, the only one in the Archipelago. With the kind permission of Mr Adam Sedgwick I had taken out with me from Cambridge a couple of drums of wire-rope, and one of these was fixed upon thwarts on the launch. Eventually I came to the conclusion that, when dredging from light craft in moderate depths, ordinary strong hemp rope is to be preferred. A pair of gun-metal bollards were screwed on to the stern of the vessel for the rope to pass over when hauling in, since, without these, the wire would cut through Australian hard wood with the greatest ease. The depth varied from thirty to seventy fathoms and there is no doubt that the result of these laborious dredgings was not very encouraging. They simply proved (apart from the chasms mentioned above) that the ground on which *Nautilus* is caught in the fish-baskets is essentially composed of volcanic mud and pumice stones.

While staying at various places about Blanche Bay my food, besides tinned stuffs and an occasional fish, consisted principally of yams in the north-west season and taro during the south-east monsoon. These invaluable tubers and corms are purchased from the women at the markets which they hold periodically on the beach. They bring

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[1] Not in all species, cf. Souleyet's figures in the Atlas of *Voyage de la Bonite*, 1836—1837.

[2] "The Fauna and Flora of Valencia Harbour," *P. Irish. Ac.* (3), v. p. 751, 1900.

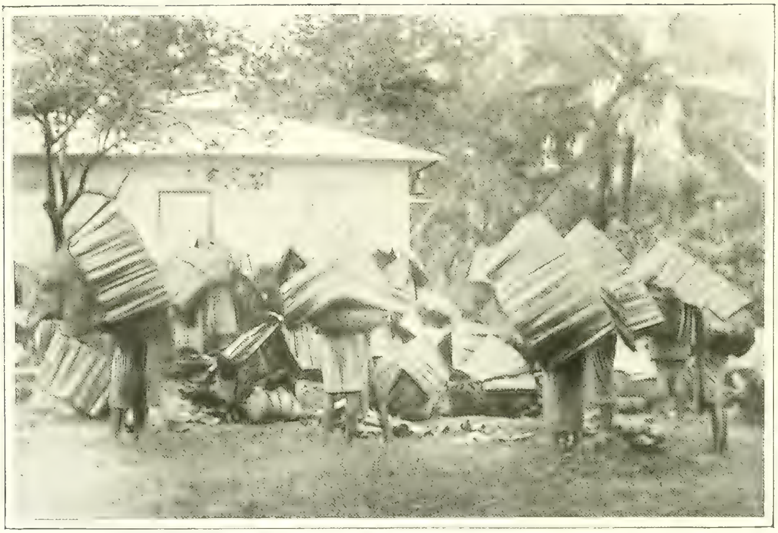

Fig. 3. Market-women at Ralum protecting themselves with pandanus rain-mats during a shower.

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down astounding loads of vegetables from their gardens in the bush, carrying them on their backs in palm-leaf baskets, the weight being supported by a band which passes across the forehead. Besides this vegetable load they frequently carry an infant as well, slung in front in a native bark-cloth fastened over the shoulders. All the infants at a certain age have their small bodies beset with numerous raised sores nearly an inch in diameter. To the inexperienced eye they present a shocking appearance at this stage, but one soon learns that the mothers cherish these sores and even, I believe, keep them open. If the sores do not break out there is cause for anxiety for the future health of the child. The markets are aboriginal institutions and are held in the bush, far from the influence of the white man, as well as on the beach.

As a general rule fish caught in the fish-baskets can only be bought with diwara, while yams and taro may be paid for with tobacco.

The natives are born traders in their own way, and liberality is likely to have a demoralising effect upon them. But their ways are peculiar, and appear at times unreasonable; in fact their actions are often quite devoid of reason, being based either upon tradition or inherited instinct or else upon some chronic, deep-seated, primary logical fallacy to which they are held in ineradicable subjection. Unfortunately besides these primal, more or less picturesque attributes, they well understand the subtleties of double-dealing and sophistry. If, for example, one applies soothing balsam to their sores, they are ready to assume that the obligation rests with the donor, unless perhaps their idea is that a little tobacco is necessary to complete the cure. On one occasion the paddles had been left for a few moments unguarded in my canoe on the beach. A passing native promptly appropriated them, took them to a neighbouring compound and had the impudence to ask for payment in response to my indignant demand for restitution.

It is not difficult to acquire a cursory knowledge of the New Britain language, which possesses simple detached particles and a straightforward syntax[1]. Of course the natives spend a good deal of their time lounging about or idly amusing themselves, and the word they use to express this pastime is "limlibur." Often during my operations in the Bay or on shore, natives whom we passed in canoes or on the beach inquired whether I was amusing myself in the sense of "limlibur."

There is no telling for how many years the *Nautilus*-fishery has been carried on by these natives. It is not a regular source of food but is resorted to when other provender is scarce. The range in size and age of the individuals taken in the fish-traps is considerable, and as the young are tender and tempting, it happened that I had some difficulty in impressing upon the fishermen that it was precisely these which I particularly desired to procure. They had no knowledge whatever of the possible egg-laying properties of the "pal-a-lialia[2]," on the contrary they scouted the idea with ridicule. This was in itself a bad sign, in consideration of the intimate and intuitive acquaintance which they manifest with many natural phenomena.

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[1] An exceedingly useful and reliable dictionary, following the plan adopted by the Rev. G. Brown for the language of the Duke of York Island, is entitled "A Dictionary of the New Britain Dialect * * * * * * * * * * also a Grammar" by the Rev. R. H. Rickards, 1889. It has not been printed, but I am informed that there is a copy in the library of the British Museum.

[2] The native name for *Nautilus*.

In New Britain the year is divided into two sharply contrasted seasons distinguished by the direction of the prevailing trade-wind. The fine south-east season lasts approximately from April to October and during the rest of the year, from November to March, the north-west wind blows almost unceasingly, bringing in its wake rain and squalls.

In other localities, such as the Moluccas and the Philippines[1], *Nautilus* can only be obtained during the time of the south-east monsoon, but Blanche Bay has this advantage, that it yields up its treasure throughout the year.

The traps which are set for *Nautilus* at a depth of from thirty to seventy fathoms are baited with small soft-skinned fishes which congregate in shoals at various points of the coast and are obtained by exploding a charge of dynamite in their midst. This will no doubt appear a reprehensible method to an angler but it should be remembered that it is the common custom, sanctioned by high and low in these parts.

On a typical occasion in January 1895, which I may describe, having procured my bait I took it to Davaun, To-vungia's village, in order to make arrangements for the setting of the traps during the coming night. I also purchased for myself a fish-basket in exchange for a "lava-lava" (waist-cloth) and six sticks of tobacco, and then returned to Vulcan Island. As soon as the fishermen who happened to be there saw that I was becoming independent of them they set to work with a will to bait the trap by tying the small fish called "malabur" on fibres purposely suspended inside from the framework. After this had been done and a heavy stone had been attached at each end the fish-trap was ready to be mounted upon a canoe and taken to the selected spot.

We baited two traps on this occasion and started out, in two canoes, shortly after sundown, paddling towards Davaun and stopping rather close to the shore opposite to a point where a light was burning at "house belong To-galli," all positions being ascertained by dead reckoning. We began to lower my basket at 7.20 p.m., using a native rattan cable, and finished paying out the rope after the lapse of twenty minutes; during this time, that is to say while the basket was slowly sinking, the canoe was kept in gentle and silent motion by the assistants.

To-kiap, master of the canoe, having made a float of light wood, set the whole thing adrift and then we cruised about until 10 o'clock when we recovered the float and began to haul up. There were no *Nautili* in the basket, a disappointment of small moment to the biologist accustomed to negative results.

A thermometer, kindly lent by Mr Parkinson, which I had taken the opportunity of fixing to my basket, showed a difference of about 9° C. between the temperature of the bottom of the bay and that of the top, the respective readings being 20° C. on the *Nautilus*-frequented ground as against 29° C. at the surface.

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[1] Concerning the occurrence of *Nautilus* at Amboyna, Dr Semon's work, *In the Australian Bush*, may be consulted. As for Negros, one of the Philippine islands, I am indebted for information to Prof. D. C. Worcester, formerly of the University of Michigan, and to Prof. Bashford Dean of the Columbia University, New York. Prof. Dean has published an illustrated account of his observations, entitled "Notes on Living Nautilus," in the *American Naturalist*, Vol. xxxv. 1901, pp. 819—837.

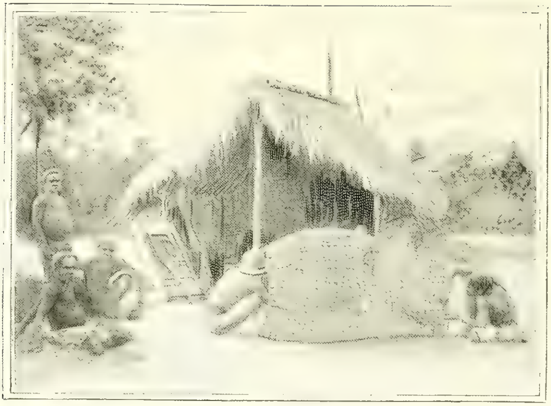

Fig. 4. Natives baiting a trap for Nautilus on Vulcan Island, Blanche Bay.

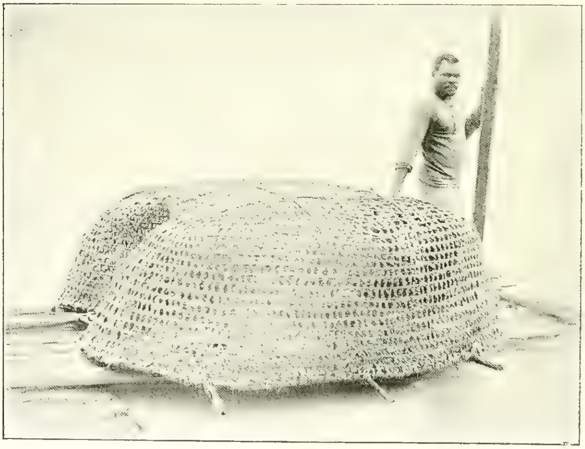

Fig. 5. Lifuan fish-trap on raft with native (Saono); the raft is moored upon the beach in Sandal Bay.

[*Photograph by Rev. J. Hadfield.*]

We then moved on a short distance until we arrived opposite "house belong To-gogi"; here we lowered once more, hauling up again shortly after midnight. This time we were fortunate in the capture of two specimens, a large mature male and an immature female. The second canoe now rejoined us in order to hand over their bag which amounted to six specimens, and we then returned to Vulcan Island. On the following morning between 7 and 8 o'clock, To-vungia came across from Davaun bringing seven more *Nautili* caught overnight.

Of the fifteen individuals procured on this occasion only two were females and this numerical disproportion between the sexes was maintained, with greater or less variation, in the subsequent takings.

One more incident may suffice to complete my description of the *Nautilus*-fishery in Blanche Bay. On January 21, four canoes, each carrying a baited fish-trap, left Vulcan Island at 5.30 p.m. to sink the baskets on the *Nautilus*-ground.

I accompanied them as before in To-kiap's canoe. Having cast off the floats we went ashore at Davaun to rest, lying down on plaited cocoa-nut leaves placed on the ground. At about 10 o'clock, a gale of wind and rain burst upon us and I adjourned, with To-mangiau and To-kiap, into the latter's house, a good weather-proof palm-leaf hut, but very small. There were already two men asleep on the ground and a fire burning in the middle. However, we went in and lay down to sleep through the gale which lasted until midnight, and it was not before 1.30 a.m. that our members were sufficiently roused to be able to set out for the purpose of raising our baskets. My basket contained six *Nautili*, and altogether the catch amounted to twenty-one, of which sixteen were males. Upon commencing to return to Vulcan Island, the clouds looked so black and threatening ahead, lowering ominously over the summits of the Mother and Daughters, that we reluctantly deemed it necessary to put back to Davaun. Accordingly we returned to enjoy the shelter of To-kiap's roof once more and hardly had we regained it when the storm-clouds broke and converted the bay, for the time being, into a howling wilderness. We had in fact just been able to haul in our traps in the interval between two severe squalls.

Just as the local inhabitants regard Blanche Bay as the source of the sea, so as I lay prone upon my mat listening to the raging of the elements it seemed to my fancy to be the very cauldron in which the north-west squalls were brewed.

Nautilus is thus trapped in the watches of the night and it is "tambu" to speak while the lines are being hauled up from the depths. At first I was liable to desecrate the performance by breaking the silence to utter some jargon of "pidgin English" or perhaps mutilated patois, but I soon learned to respect the unwritten law.

The fish-baskets are large barrel-shaped contrivances made by interlacing bamboo-slips bound together by rattan fibre. They are five or six feet in length and three or four feet across the middle; they are furnished at each end with an inverted funnel terminating in a forest of loose slips which lie across the inner mouth of the funnel and, while not preventing the entrance of various marine animals such as *Nautilus*, fishes, sea-urchins and crustacea, effectually foil their attempts to escape.

The construction of these fish-traps varies in certain particulars of minor importance although carefully considered by their makers. When not in use they are stored away by being suspended from the overhanging stems of the cocoa-nut palms which fringe the beach, and consequently they are a conspicuous feature in the shore scenery. The best of them are employed for surface-fishing during the south-east season; for this purpose they are attached to large bamboo floats which are held in position by anchors made by enclosing heavy stones in a rattan cage. When once they are placed in position these anchors are never moved and frequently my dredges brought up lengths of former rattan cables which had become water-logged. In the course of time these anchor ropes become coated with Hydroids and also serve as a resting-place for Annelid worms (especially one handsome species called *Amphinome rostrata*). Sometimes grape-like bunches of Cephalopod eggs are found attached to them. Thinking that *Nautilus* might use them for this purpose I once requested the Rev. W. J. Chambers of the Wesleyan Mission to use his influence to induce certain natives to allow me to haul up two or three of their anchors, but the result was negative.

The opening of the fishing season, when the natives go out in their white canoes to lay their anchors and set their traps, is a joyous occasion and is heralded by the blowing of *Triton* conchs.

The squid egg-clusters referred to above are called "a mo a tauka" and I made special inquiries of the natives to ascertain whether they were acquainted with "a mo a pal-a-lialia." They replied No with emphasis ("pata-na") as if incredulous of their existence. This was sufficient to convince me that the eggs of *Nautilus* are not deposited in obvious bunches or in ordinary situations.

When living *Nautili* are confined in a vessel of water, numbers of small crustacea issue from the mantle cavity in which the gills lie and also from the funnel by the pumping action of which the shell is driven backwards when the animal is swimming freely. These ectoparasites apparently live upon the slime which is secreted from the mucous surface of the body, and, on leaving their host, swim about actively in the water and also cling tenaciously by means of a peculiar suctorial apparatus to the sides of the vessel[1].

In the month of February (1895) I gladly accepted an invitation from Mr Parkinson to accompany him on a short recruiting voyage to New Ireland and New Hanover in a small 50-ton fore-and-aft schooner called the Mayflower.

There was the possibility that a locality might be found where *Nautilus* could be investigated in shallower water than in Blanche Bay. But these countries are too wild and no reliable information could be obtained. The journey was, however, interesting in itself as providing a glimpse of native systems with quite a different code from that by which the inhabitants of New Britain are bound, notwithstanding the fact that the islands form part of one and the same compact archipelago. The distances are too great for small canoes to traverse so that there is practically no regular communication between New Britain and the larger islands except the Duke of York Island. Moreover the natives are suspicious not only of the white man but of their own colour.

Between New Ireland and New Hanover there is a labyrinth of islands and channels, one of the islands when seen from the west presenting a symmetrical appearance with a flat-topped mountain in the centre, which has suggested the appropriate name of Mausoleum Island.

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[1] They are named *Anchicaligus nautili* by Mr Stebbing, Part v. pp. 667 and 668. For an account of Crustacean ectoparasites of other Cephalopods see Wierzejski, A., "Ueber Schmarotzerkrebse von Cephalopoden," *Zeitschr. wiss. Zool.*, Bd. 29, 1877, p. 562.

The opening at the top of the New Hanover and Mausoleum Island canoes was very narrow, the cavity of the canoe widening out inside; the outrigger was adorned with pigs' tails. Some of the natives had a wild hunted expression in their eyes such as I had not seen elsewhere; one fellow was decorated with a lurid red pigment on chest, shoulders, back and thighs. Whether this was for mere display or to produce a terrifying effect, I do not know. On the upright pole of the outriggers there was occasionally a *Nautilus* shell, no doubt placed there as an object of beauty, the natives being very susceptible to singularity of form, although the shell is also used for the more commonplace function of baling out the canoes. Many of the canoes only came within shouting distance, their crews being doubtless smitten by their consciences on account of former delinquencies and afraid to come alongside. Higher up along the coast of New Hanover we went ashore and engaged the bulk of the boys, the natives being used to the recruiting business.

The parts visited on this occasion included the whole south-west of New Hanover and along the north coast round Cape Charlotte as far as the island of Kung, one of the North Islands, where there was a trader's station. On the return journey we passed through Steffen Strait as far as the island of Nusa and Cape Nowon on the mainland of New Ireland.

The men of New Hanover go about in a state of nature, carrying wooden spears either singly or in sheaves. Some of them wear armlets of closely woven fibre which sometimes become so tight, with increasing age, as to be almost concealed below the neighbouring folds of flesh. They also wear spindle-shaped, well-fashioned rods of shell passed through the nasal septum, just as in New Britain some of the better class of bushmen employ quills from the cassowary (*Casuarius bennettii*) as nose-sticks. Occasionally one sees a man wearing a large white disc cut out of the giant clam *Tridacna* and suspended by a string round the neck, forming a kind of medallion varying from two or three to five or six inches in diameter. This ornament (called "kapkap") is more frequently met with in New Ireland and is generally much improved by the addition of a circular lamina of tortoise-shell beautifully fretted, the whole forming an artistic composition, the tortoise-shell plate being thrown into elegant relief by the white background furnished by the *Tridacna* shell-disc.

Armlets made by cutting out segments from large *Trochus*-shells are commonly worn by well-to-do women throughout the Bismarck Archipelago. But the woven armlets mentioned above serve a double purpose, decorative and utilitarian, since all kinds of things, such as a pipe, a stick of tobacco, ornamental leaves and so forth can be carried thrust in between the ring and the flesh.

The women of New Hanover and neighbouring islands wear very curious hats made of pandanus leaves, called "kabil," which they are unwilling to remove in the presence of men. When I first saw women running along the shore to meet the boat, I was greatly fascinated by this singular head-gear which somewhat resembles a bishop's mitre. The scenery in New Hanover is very attractive and is not rendered less so by the native taro plantations in the form of terraces on the sides of the well-wooded hills, with palms and Cycads in the foreground. They use long, light, narrow rafts made with the midribs of sago-palm leaves lashed together and propelled with simple bamboo rods. When a crowd of natives came to the beach the women kept together in a separate group, and when a young fellow accepted the recruiting terms and was taken away in the boat the poor women often raised a terrible wail, shrieking, stamping and rubbing sand over their bodies. But from previous experiences I felt that such grief would be soon assuaged, heart-rending though it appeared.

The wearing of the "kabil" is an act of deference to the men. In one village called Neila-as, on the island of Kung, there was a tree near the chief's house, upon which several skulls were exposed, with huge rents behind the ear. There can be no doubt that in this country infringements of the social code are visited with swift retribution.

At Neila-as we wanted to photograph a group of the women with their kabils, and in order to place them in a favourable light it was necessary for them to cross the village-square. I was much interested to observe that they crossed this space on their knees in view of a group of men who were watching them.

Birds are "tambu" or sacred in New Hanover and each individual native acknowledges a certain kind of bird as his patron-bird and the people range themselves accordingly into groups or phratries, named after the birds. The esteem in which birds are held is further manifested in their carvings, particularly in the figure-heads of their canoes which are carved out of the same piece of wood from which the dug-out itself is made; the head and eyes are usually distinct but the rest of the body is drawn out into a fantastic scroll and in fact the whole figure of the bird may degenerate into a decorative scroll. Another kind of carvings representing birds is called "kui." This is used in dances and is provided with a spatula-shaped basal piece by which it is held in the mouth; the eyes are the blue opercula of *Turbo petholatus.*

Seismic disturbances are of frequent occurrence in New Britain and when they occur at night the bush re-echoes with the blowing of conchs and the tattoo of "garamăts" or native tomtoms, to soothe the angry spirit. If there were any houses built of stone the earthquakes would no doubt frequently be classed as disasters, but under present conditions only minor casualties occur such as the upsetting of lamps and other household implements.

In the Strait of Rakaiya between Vulcan Island and the mainland, both men and women used to come down to scoop up the black sand or mud near the shore with small hand-nets in search of the "diwara" shell which occurs here in small quantities but is said to be of inferior quality[1], and varies in colour from almost pure white to jet-black. The natives sift the sand through their nets and each shell, as they find it, is carefully stored away in their mouths until their jowls are full.

Finding it necessary to have some lighter craft than a whale-boat for general purposes, and not being able at that time, for reasons stated above, to purchase a New Britain canoe, I commissioned a Samoan mission-teacher to make me a canoe in Samoan fashion during his spare time. In this plain unadorned dug-out I was able to traverse the whole extent of Blanche Bay with a single companion. When it sprung a leak, as all canoes do sooner or later, the holes were stopped up with the bruised fruit of a tree

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[1] The principal source of the shell lies far away on the north coast in the district of Beining.

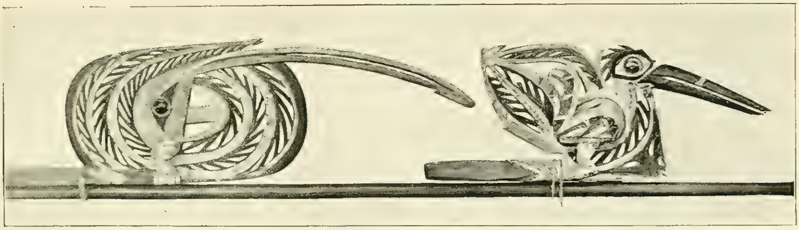

Fig. 6. Bird-scrolls ("kui"), New Hanover.

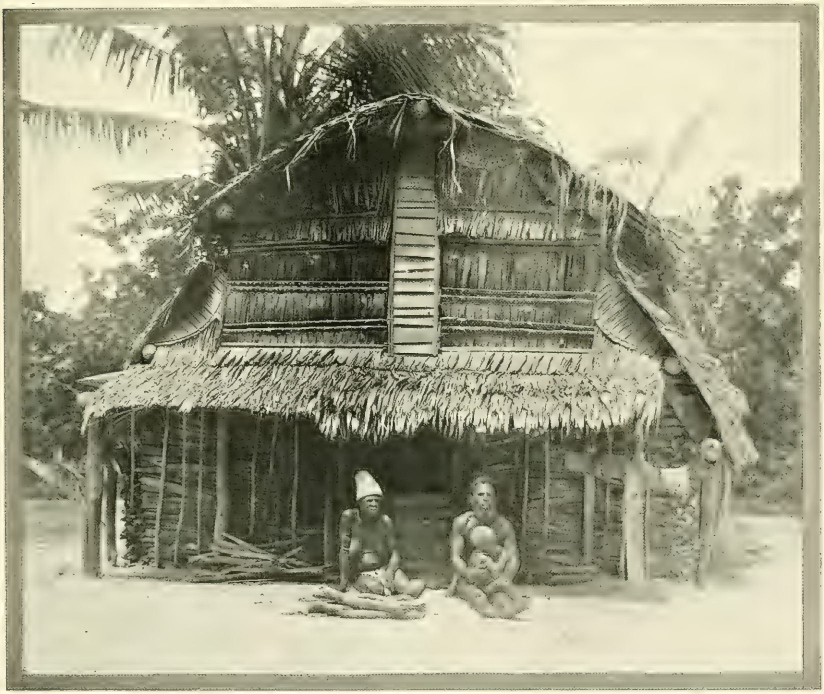

Fig. 7. Domestic scene at the village of Neila-as, New Hanover.

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called "a tīta" (*Parinarium laurinum*) which has a wide distribution and is even called by the same native name in the Solomon Islands, where it is employed for the same purpose and also as cement for the remarkable inlaid work which the Solomon Islanders practise in the decoration of their canoes, paddles and weapons.

The kernel of the nut is removed and rubbed against a stone to produce a pulp. According to native directions "u na ud ia ta ra wat," which means, word for word, "you must rub it on the stone," the particle "na" implying both obligation and futurity. A quantity of dust or ashes is mixed with the pulp to form a paste which is then employed like putty in filling up the crevices of the canoe. The composition soon turns brown and dries hard, after which it is plastered over with lime obtained from calcined corals and mixed with the expressed juice of the cocoa-nut.

The natives are cynophagists and I was told that they rub the bruised fruit of the *Barringtonia speciosa* called "a vutun" on the closed eyes of recently born pups, to cause them to open, but I did not actually see this veterinary feat performed.

I stayed at Karavia, renting about half a bungalow belonging to Ah Tam of Matupi, from March 1 to July 12 (1895). During this time hardly a day passed without some experiments, operations or observations relating to *Nautilus* being carried on. If I made an excursion into the bush behind Karavia to shoot a pigeon for lunch or for change of occupation, either a cage, barrel, basket or hempen tangle would be testing its quality in the silent depths of the bay.

It was during one of these excursions, on the occasion of my second visit to New Britain, that I had the good fortune to come across a species of *Peripatus*. At the outset of my journey I had calculated upon the possibility of discovering the *Peripatus* of New Britain, but it was not until near the close of my voyages, in the year 1897, that my dream was realised.

It is well known that *Peripatus* occupies an isolated position in the animal kingdom, presenting signs of affinity both to the Annelid Worms and to the Tracheate Arthropods but not falling into the sequence of normal gradation of forms. When seen from above, immediately after turning over a stone or a fallen leaf or a piece of rotten bark, it resembles a caterpillar; if looked at from below it is like a centipede with many pairs of clawed legs, and when held in the hand or between the fingers it is found to be soft like a caterpillar or a worm.

From a zoogeographical point of view, *Peripatus* possesses a perennial interest which does not diminish as time goes on, although the recent discovery of a new genus, with three new species, in the Malay Peninsula during the Skeat Expedition to this region, renders generalisation for the present impossible. We may confidently await further additions to our knowledge of the distribution of the *Onychophora* for many years to come, according as the various islands of the Eastern Archipelago are searched for their cryptozoic inhabitants. For example it may seem difficult to believe that *Peripatus* has been overlooked in Java which has been visited by so many naturalists of the highest distinction, but it is equally incredible that it does not occur there. It is to be looked for under leaves, bark and stones in damp mountain valleys near streams or springs, and its absence from the neighbourhood of one source does not preclude the possibility of its occurrence near another half-a-mile distant. It is essentially a creature of contradictions both in its structure and habits. While abundant moisture is absolutely indispensable to its existence, immersion is quickly fatal; it is therefore likely to prove of peculiar theoretical value to the zoogeographer since the only conceivable means of transit from one place to another is by land. But the occurrence of distinct genera in Australasia (Australia, Tasmania and New Zealand), in New Britain and in the Malay Peninsula and Sumatra, renders it impossible, in the absence of information concerning the representation of *Peripatus* on any of the intervening islands, to construct a scheme of any route of migration in former geological ages, especially as we cannot be certain whether the centre of distribution lay in the Eastern or the Western Hemisphere, although M. Bouvier[1] is of opinion that the American Continent was the original head-quarters of the Onychophoran stock.

Until quite recently a peculiar correlation has seemed to subsist between three classes of phenomena in their relation to *Peripatus*, namely: (1) the discontinuity of its areas of distribution; (2) the generic divergence of the different types; (3) the method of nutrition of the young in the intra-uterine development.

It now appears certain that this correlation is neither so simple nor so fixed and definite as had been supposed. If the method of embryonic nutrition, for example, were strictly correlated with the generic divergencies, the selection of any particular method as bearing a more primitive or ancestral stamp than the rest, might well appear arbitrary, since the generic divergence may be taken to depend partly upon the discontinuity of distribution.

When I first became acquainted with the blastodermic or trophic vesicle of the embryos of the New Britain species (*Paraperipatus novae-britanniae*) I was completely at a loss to offer any provisional explanation of it based upon morphological principles, but in the course of time I evolved a working hypothesis, an account of which was published[2].

Through the kindness of Professor G. B. Howes, F.R.S., I have recently come to the knowledge of an interesting memoir by Dr H. J. Hansen of Copenhagen, on the structure and development of a primitive insect named *Hemimerus talpoides*, belonging to the order Orthoptera[3]. This insect has been found living in the fur of a West African rat of the genus *Cricetomys*; it resembles a wingless cockroach in superficial appearance but is more nearly related to the *Forficulina* than to the *Blattina*, as is indicated especially by the arrangement of the mouth-parts. The chief peculiarity of *Hemimerus* lies in its anomalous method of propagation which isolates it from all known insects. It is truly viviparous (not merely ovoviviparous) and in one female Dr Hansen found six embryos at different stages of development, the largest of which, in its convoluted state, measured 2·8 mm. in length and the smallest 1·2 mm.[4]

Dr Hansen points out that it is thus evident that *Hemimerus* gives birth to its young singly and in succession, not simultaneously; moreover the newly born young only differs from the adult in the less number of joints of the antennae and in lacking the sexual modification of the posterior abdominal segments.

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[1] *Zool. Anz.* xxiv. 1901, p. 59.

[2] Willey, A., "Trophoblast and Serosa." A contribution to the morphology of the embryonic membranes of insects. *Quart. J. Micr. Sc.*, Vol. 41, 1899, pp. 589—609.

[3] Hansen, H. J., "On the structure and habits of *Hemimerus talpoides* Walk.," *Entomol. Tidskr.* xv. Heft 1, 1894, pp. 65—94, Pls. 2 and 3.

[4] The length of the parent without the cerci was 11·5 mm. [Hansen.]

In the four largest embryos which he extracted from the uterus, Dr Hansen observed a most remarkable feature. From the articular membrane which connects the head with the protergum, there issued an unpaired nuchal organ, slender at the base but rapidly increasing in volume, which became lacerated during the removal of the embryo. "This organ," he considered, "must be in connection with the interior wall of female genital organs and thus serve the nutrition of the young ones."

While taking out the two smallest of the embryos, which he was able to procure without destroying the specimen, the head was broken off in each case, which seemed to him to indicate "that also these specimens had been fixed by an organ from the neck." Remarking upon the probably nutritive function of this nuchal organ, Dr Hansen does not hesitate to give it as his opinion that the very anomalous mode of propagation of *Hemimerus* is of great systematical importance[1], and marks it as the type of a distinct family allied to the *Forficulina.*

To my mind the nuchal organ of *Hemimerus* is homologous with the corresponding trophic vesicle of *Paraperipatus novae-britanniae* as described by me[2], all that is wanted to complete the comparison being an account of the actual history of the organ in *Hemimerus* in order to demonstrate its relation to the normal embryonic membranes of the insect.

The other fact which it is my fortune to bring forward in support of the suggestion that the trophic vesicle here referred to is a formation of primary or phylogenetic significance, is due to the recent observations of M. Bouvier of Paris[3]. In a species of the South African genus *Peripatopsis*, namely, *P. sedgwicki* Purcell, M. Bouvier describes a blastodermic vesicle with nuchal insertion as in *Paraperipatus.* The vesicle attains relatively enormous dimensions, measuring as much as 5 mm. in length in the case of an embryo of 3 mm. M. Bouvier is of opinion that the species in question is the most primitive member of the genus *Peripatopsis* and that the other species of this genus, as regards their development, are derived from it by atrophy of the vesicle accompanied by greater simultaneity in the growth of the embryos.

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[1] The expression "great systematical importance" may be interpreted in various ways, but, for my part, I prefer to take it as signifying great phylogenetic importance.

[2] Willey, A., "The anatomy and development of *Peripatus novae-britanniae,*" *Zool. Results*, Part I. 1898.

[3] Bouvier, E. L., "Observations sur le développement des Onychophores," *C. R. Acad. Paris*, tome 131, p. 652, 1900. M. Bouvier has again returned to this question ("Sur la reproduction et le développement du *Peripatopsis blainvillei,*" *op. cit.*, tome 133, p. 518, 1901) in connection with the Chilian species which affords a transition from the Andicolous to the South African forms. He finds that the genus *Peripatopsis* presents three modes of development:—1. avec un œuf très petit et sans annexe embryonnaire (*P. blainvillei*); 2. avec un œuf assez volumineux et [avec] vésicule nuquale (*P. sedgwicki*); 3. avec un œuf assez volumineux et sans annexe embryonnaire (tous les autres *Peripatopsis*). In the second category I have placed the word "avec" in square brackets, because, in the original, the word "sans" is inserted by an obvious typographical error.

That all these deductions cannot be accepted without discussion goes without saying, but fortunately the issue is fairly clear and an important presentation of the opposite view has quite recently been contributed by Professor Arthur Dendy ("On the oviparous species of Onychophora," *Quart. J. Micr. Sc.*, Vol. 45, 1902, pp. 363—415, Pls. 19—22). Dendy thinks that the oviparity of certain Australian species which lay large yolk-laden eggs is primitive, and adduces in support of this contention the consideration that the chorion which surrounds the intra-uterine embryo in the viviparous species of *Peripatus* may be regarded as a vestigial structure inherited from oviparous ancestors in which a chorionic membrane acted as a protection to the deposited egg during the early stages of development. It does not follow however that the eggs were primitively overloaded with yolk, since most so-called alecithal eggs are also protected by a chorionic or vitelline membrane.

I desire to take this opportunity of qualifying my former statements concerning the structure of the endoderm in post-natal and in prae-natal (*i.e.* immediately prior to birth) stages of *P. novae-britanniae* (Part I. *Zool. Results,* pp. 29 and 30). This seemed to afford ground for comparison with certain histolytic phenomena which have been observed to take place in the intestine of insects and some other animals. In his recent detailed description of the Malayan genus *Eoperipatus* (published in the *Quarterly Journal of Microscopical Science* (1901), Vols. 44 and 45), Mr Richard Evans finds no confirmation of the observations which I recorded, and gives reasons for supposing that the appearances were the result of the method of preservation. After renewed consideration and re-examination of my preparations I have come to the conclusion that he is probably right. This qualification has no reference to the "trophocytes" which I described in an earlier stage (*op. cit.* p. 22), to which I adhere.

Being desirous, as occasion offered, of acquiring some personal acquaintance with one or two of the native sorceries I brought my mind, in the Easter of 1895, to consent to be initiated into the mystery of the "pepe." The details had been very kindly arranged for me by Mrs Parkinson by negotiation with a native petty chief named Taipuk.

From information which Mrs Parkinson[1] obtained from the natives, the "pepe" is somewhat vaguely described as a preparation made by native doctors to be partaken of by others for the purpose of causing the spirits which dwell in certain trees to enter their bodies for specific purposes. There are several trees which are frequented by the spirits, notably the banyan tree, "a giau."

The "pepe" is prepared once a year during the south-east season when it is dry, because in north-west weather the spirits are driven from the trees by the rain. At the right time, as ascertained by the behaviour of the tides, the man who prepares the "pepe" scrapes the aromatic bark from certain trees, adds to it Areca-nut and lime, and wraps the whole in the "Aier" or betel leaf, making a number of small bundles which he spreads out in the less frequented parts of the bush. When the "pepe" is laid out in this way, *i.e.*, in the manner of a repast, the people who intend to partake of it gather round it and the master gives each communicant a small parcel. They eat their parcel and then fall down in a trance as if intoxicated, and go to sleep on the spot. When they awake in the morning, they start off by twos or threes to find the spirit-haunted trees, and to sleep under them until they discover by the nature of their dreams a tree inhabited by a good spirit, *i.e.*, a male spirit, as the female spirits are reputed bad. The information which they desire to obtain from the good spirit relates to personal ornaments, waistbands made with shells, chaplets, tattoo-marks, feather-tufts for the head, scented leaves for the neck, dyes for the hair, pig's bristles for the hair, cassowary quills and opossum-teeth for the nose, painting of the body and so forth. Further information is desired upon the important matter of charms, chiefly of the nature of love-philtres, fern-seed and rain-making. All this knowledge is imparted by the good spirits in dreams to him who has taken the "pepe." The spirits have different names and different functions. One is called "Tutana Vuragit" and is described as the everlasting spirit; another is "Pepe tuna" or the true spirit of the "pepe"; and there are others. After a certain lapse of time the "pepe" votaries gather together in a special "pepe"-house to recount their visions, and then decorate themselves according to their respective inspirations. Revelations concerning future events, such as dances, are held in abeyance until the appointed time.

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[1] Mrs Parkinson was kind enough to present me with a description of the "pepe" which she reduced to writing for the occasion. The general account which I give in the text is largely derived from this document.

While holding communion with the spirits which dwell in trees, when a man, under the influence of "pepe," "exempt from public haunt, finds tongues in trees," he does not associate with his friends, but keeps in retirement until finally the maker of the "pepe" gives a great feast for the men, towards the expenses of which each guest contributes a yard of diwara, and the spell is broken.

I took my "pepe" in a secluded spot in the cocoa-nut plantation behind Ralum, but it was unconvincing, as they were afraid to give me too much "pepe," and I failed to seek subsequent inspiration under the proper trees. Nevertheless the ceremony of the "pepe" undoubtedly presents many features which are both quaint and picturesque.

I was expected to contribute to the repast a native dish called "a ku," which my boys prepared. This consists of the juice squeezed out from the white kernel of the cocoa-nut, which is boiled in banana leaves by placing heated stones in it. Under this treatment the milky juice becomes as thick as porridge, leaving a watery residue which is drained off. The creamy decoction was then tied up in the leaves and carried to the rendezvous, accompanied by a fish of moderate size, which had also been cooked and wrapped in leaves. The "pepe" was tastefully arranged on the ground in a circle, placed upon leaves with the margins artificially coloured red, and, outside these, wreaths of similar leaves, and also variegated leaves of *Dracaena*, *Croton*, and other ornamental plants cultivated expressly for such occasions by the natives. The whole was protected by a fane of palm-leaves. After I had paid my initiation fee of two fathoms of diwara the palm-leaves were removed, the pepe exposed and handed round. When taken, the leaf with its red-coloured margin is wrapped round the mixture of bark-scrapings and nuts, and the entire bolus is then swallowed, a taste of ginger predominating. They had prepared some six or eight leaves, which were distributed among as many persons including myself, but they said that the whole quantity prepared should have been eaten by one recipient, in order that its effects might be appreciated. The painted leaves used at the "pepe" and on other occasions are carefully hidden away afterwards so that they may not be looked upon by the women.

Shortly after the experience in practical folk-lore which I have described, namely on April 17th, 1895, Mr Parkinson invited me to accompany him to a place some miles distant in the bush behind Ralum, where a great dance or "malagĕne," called the "maravot," was going to be held. It had been convoked by an aged chief of wealth and fame, named To-ragăt, the richest and most renowned personage of all the country round Ralum.

The "maravot" is an elaborately concerted festival designed for the purpose of initiating the young men into the tribal usages, and touches the very heart of the native society of the Gazelle Peninsula. It is not held annually, but at long intervals, and like all such tribal assemblages of people who do not possess written records to give authority to their precedents, its scope will become narrowed and it will sooner or later cease to exist. I may therefore esteem myself fortunate in having witnessed this rare scene under conditions which enhanced its ethnological value and human interest.

It has been fancifully suggested by various authors of books of travel that the Papuans and other races similarly situated are relict types of the Stone Age, since in their ignorance of iron and metals generally, they are dependent upon stones and organic productions (shell, bone, wood, fibre, leaves) for their martial and industrial implements. It is therefore impossible to avoid a feeling of regret when we reflect upon the sure approach of the relentless wave of destruction which will engulf all these neolithic rites.

The accessory incidents of the "maravot," the *mise-en-scène* and appurtenances, if described in too great detail would appear sordid, perhaps even repulsive. But if it be regarded sympathetically as a manifestation of racial sentiment, its importance becomes at once evident, and one who has recently received his baptism of "pepe" should be able to approach the "maravot" in the proper spirit[1].

At the place of meeting, on the occasion of our visit, there was a large oblong enclosure fenced in by tall, opaque screens of plaited palm-leaves so as to exclude the gaze of the women to whom it is "tambu." Nevertheless, at a little distance from the enclosure there was a "monstrous regiment of women" bringing large bundles of food, called "magít," wrapped up in banana leaves. Beyond a few armlets and necklaces of *Cuscus*-teeth (which are worn alike by both sexes) the women had not decked themselves out, and they presented a rather monotonous sea of faces, as they sat on the ground smoking, chatting and chewing, while their male relatives attended to the more serious duty of dancing in the sanctuary.

The men (with the exception of the great chief To-ragăt, who came quite plain) had decorated their persons with all the ornaments which the country yields, their toilette being completed by a head-dress consisting of a tuft of white tail-feathers of the domestic fowl. Many of them had painted the body, face and hair with red, white and black native pigments, and some were actually green with smeared lichen. The wealthier individuals wore precious collars of *Cuscus*-teeth, nose-pieces and chaplets.

At one end of the enclosure there were some remarkable mural paintings representing figures of reptiles with human heads, forming an appropriate mounting for the piece; at the opposite end, faced by the natives while dancing, there was an exhibition of coils of diwara belonging to various chiefs, this in itself being a sufficient proof of the solemnity and sincerity of the occasion.

When advancing to take their places in serried ranks within the sacred precincts, where they presented the appearance, viewed from an elevation, of a bed of white feathers, the men formed processions in single file, chanting as they walked and carrying coloured leaves and carved devices. One very large figure representing a departed chief,

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[1] In the dictionary of the New Britain dialect by the Rev. R. H. Rickards, to which I have already made reference, the "maravot" is defined as the ceremony and dancing initiatory to the "igiăt" (pronounced "ingiăt"), which is, as far as I could gather, a secret fraternity which most of the men join in order to settle their accounts in this world and the next to the best advantage. I think it might be possible to compile a connected account of the native economy of this part of New Britain based upon the "igiăt," elucidating all the ceremonies and periods which precede membership and all the privileges and powers which ensue.

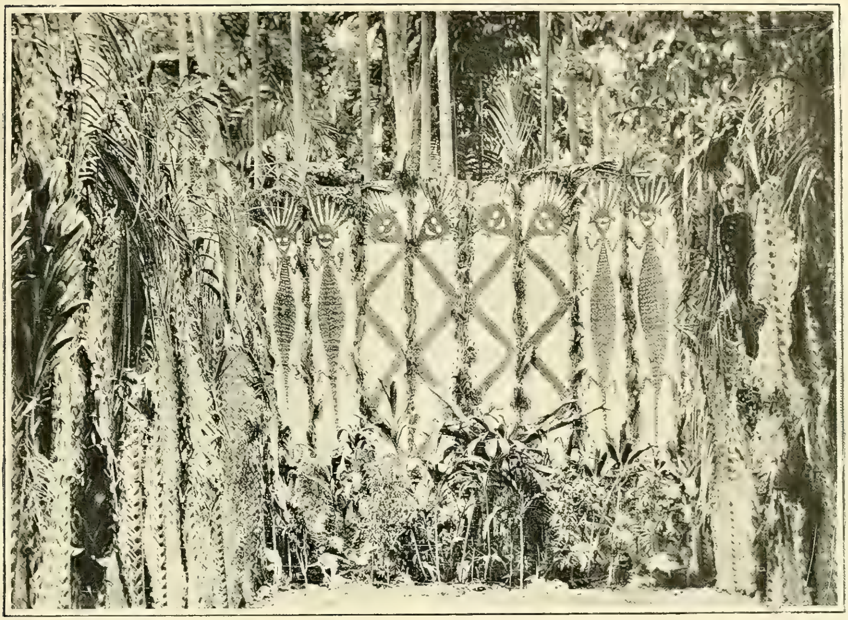

Fig. 8. Screen-paintings within the maravot enclosure (New Britain).

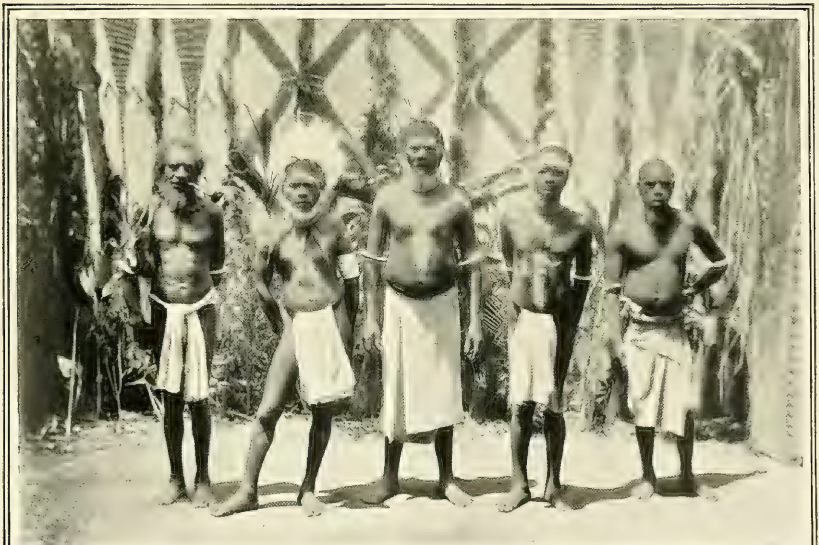

Fig. 9. Natives who took part in the maravot. The central figure is a petty chief (Taipuk) who like his two neighbours wore a collar of Cuscus-teeth.

To face page 708.

had a head consisting of a human skull covered with dark plastic material ("a tita") and was also adorned with a *Cuscus*-necklace. As the procession passed along, the women raised a howl, perhaps bewailing departed spirits. The life-size human emblem and another smaller one were placed in front of the diwara, facing both the performers and the altar-piece at the far end.

Some of the dancers brought very curious carvings representing a tongue protruding through an open mouth. These were placed upon a rough log bench immediately in front of the altar-piece, and I inferred that they symbolised spirit-tongues, but have no information on this point.

The actual "malagĕne," in the densely crowded enclosure, consisted of an interminable medley of unintelligible but well-rehearsed incantations delivered by one or other of the assistants in a high-pitched voice and followed by a chorus of responses, shouts and chants, all in unison, accompanied by dancing and some comedy. Each distinct dance was inaugurated by the entire company, at one moment, blowing out from their mouths a cloud of betel juice into the air, an operation known as "puruk." As I have already indicated, the bulk of natives, constituting what I may term the chorus, faced the diwara with their backs to the altar-piece, but the leaders, first among whom was the venerable To-ragăt, faced the crowd and appeared to direct the performance.

Some of the young novitiates, sons of chiefs and valiant men, gifted with superb figures and well-chiselled features, commanded instant admiration; but the older congregants improved on acquaintance.

Among the lower orders of marine animals to which I devoted some attention while dwelling on the shores of Blanche Bay, two or three species of Ascidians deserve special mention on account of some striking circumstance of habit or structure.

I have described one of these under the name *Styeloides eviscerans*[1]. It has a very characteristic form, colour and encrusting method of growth which distinguish it from all the remaining somewhat numerous species which I observed during my entire expedition. It also differs from other Tunicata by the readiness with which it throws out its entrails, in a manner analogous to the evisceration of some Holothurians, shortly after removal from its natural surroundings. The extrusion is effected by successive contractions of the atrial siphon, and if the tunicary be cut open there is found to be no trace of lesion inside. Moreover the animal appears to be perfectly healthy and normal externally after having got rid of its viscera, and both the buccal and the atrial siphons remain sensitive to mechanical and chemical stimuli.

I found a few examples of this species attached to the lower surface of stones off the south-west shore of Vulcan Island at a depth of one-half to one fathom. The general colour is a dull reddish-brown, more pronounced near the apertures, the margins of which are dark red, interrupted by four light streaks indicating the characteristic quadripartite nature of the siphons. Individuals occur singly and associated in groups, in which case they may be so intimately united by fusion of the test-substance that one would be tempted to assume that the group represents a colony of ascidiozoids budded from a parent stock. There is however, so far as I could ascertain by dissection, no organic union.

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[1] Willey, A., "Letters from New Guinea on *Nautilus* and some other organisms." *Quart. J. Micr. Sci.*, Vol. 39, 1897, p. 161.

Why one species should act in the way described while another attached perhaps to the same stone does not, is a question not easily answered, but the fact affords a special case of self-mutilation or autotomy, a phenomenon of wide distribution in the animal kingdom, varying greatly in its manifestations.

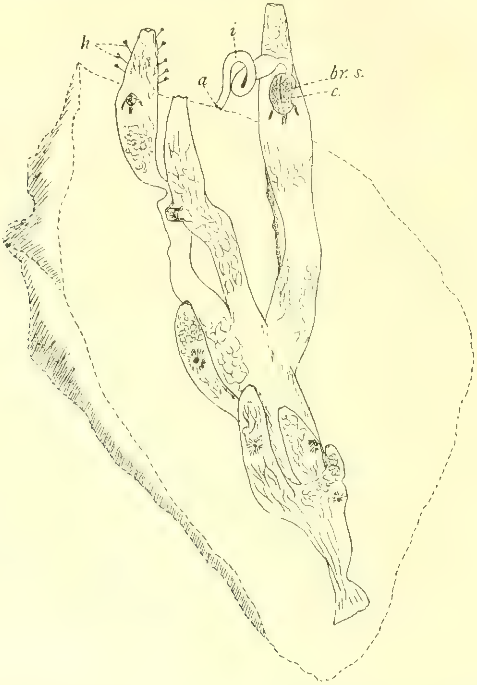

FIG. 10. Group of seven individuals of *Styeloides eviscerans*, represented as lying attached to the surface of a fragment of stone. In the large individual to the right the digestive tract is indicated in process of extrusion through the atrial aperture. *a*. Anus with frilled margin. *i*. Intestine. *br. s*. Branchial sac. *e*. Endostyle. *h*. Foreign organisms attached to test. (From *Quart. J. Micr. Sci.*, Vol. 39, 1896.)

The genus *Styeloides* was established in 1885 by Dr Sluiter[1] for a species found by him near Batavia, which appeared to be normally destitute of a branchial sac. Subsequently he returned to the subject and suggested that the branchial sac and intestine are lost in the adult period only[2].

[1] *Natuurk. Tijdschr. Nederl. Ind.*, Bd. 45, 1885, *Styeloides abranchiata*, Sluiter.

[2] Sluiter, C. Ph., "Tunicaten." Semon's *Zool. Forschungsreisen*, v. 1895, *Styela solvens*, p. 182.

More recently Dr Sluiter has accepted my observations as affording an explanation of the absence of the branchial sac in *Styeloides*, and he thinks that this generic name should lapse in favour of *Polycarpa*[1].

Another noteworthy Ascidian which I found in Blanche Bay on a reef-patch off Baravon, is called *Rhodosoma huxleyi*, and was described under the name *Pera huxleyi* in 1862 by Dr J. D. Macdonald, who obtained his material from the Bellona Reef[2]. The peculiarity of *Rhodosoma* is this, that the upper portion of the test fits like a lid upon the rest of the tunicary and can be raised and depressed like the valve of a lamellibranchiate Mollusc. Compared with those bivalve Molluscs where one valve is fixed to the substratum, the action of the lid of *Rhodosoma* which protects the siphons bears a striking analogy to that of the freely hinged valve of the former. It is, in fact, a good example of parallel evolution, a phenomenon of wide occurrence and profound significance, but not always easy to recognise. By what may be termed a singular coincidence, the late distinguished Professor H. de Lacaze-Duthiers[3], who was one of the first to publish a full account of *Rhodosoma*, was at great pains to demonstrate the supposed molluscoid affinities of the Ascidians, and the discovery of a species of this peculiar valvate genus confirmed him in what most naturalists will now admit to have been an interesting and instructive error.

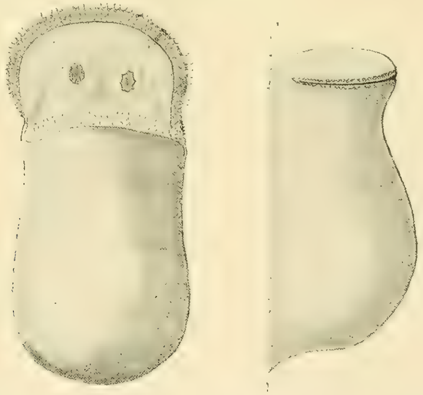

Fig. 11. *Rhodosoma huxleyi*; front view with operculum raised; side-view with lid closed. (Semi-diagrammatic, partly after Macdonald.)

Finally there is a third Ascidian which is abundant in Blanche Bay and neighbouring localities (New Guinea, etc.) and claims notice on account of its size and brilliant orange hue but more especially on account of the remarkable fragmentation of the dorsal tubercle (orifice of the subneural gland into the branchial sac) which appears as a large number of irregularly placed apertures occupying a triangular area. This very curious species is the *Ascidia aurata* of Quoy and Gaimard, who gave a coloured figure of it in their work on the zoology of the Astrolabe[1].

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[1] Sluiter, C. Ph., "Tunicaten von Sud-Afrika." *Zool. Jahrb. Syst.* XI., 1898, p. 5. It is not known whether the viscera can be regenerated, but Dr Sluiter thinks he has found indications of a regeneration of the endostyle in *Styeloides abranchiata*.

[2] Macdonald, J. D., "On a new genus of Tunicata (Pera) from the Bellona reefs." *J. Linn. Soc. Zool.*, VI. p. 78, 1862. I am not acquainted with any later record of this species.

[3] Lacaze-Duthiers, H. de, "Sur un genre nouveau d'Ascidien (*Chevreulius*)." *Ann. Sci. Nat.* (5) IV. 1865, p. 293. The name *Rhodosoma*, which takes priority, was introduced by Ehrenberg in 1828.

My enthusiasm for the Ascidians resulted in temporary disablement for the best part of a week, owing to the combined action of the sea-water and the heat of the sun, which so blistered my back that I experienced a complete ecdysis of the dorsal integument.

On May 6th, 1895, I took over by purchase a stout cutter-rigged sailing-boat built by Ah Tam, the enterprising Chinaman of Matupi, with whom I had been negotiating for some time. I was delighted with the new sails and the bamboo-boom and with the prospect of being able to trawl at will[2].

There was, however, ground for considerable anxiety as there was more or less constant danger of the boat being stolen by deserting labour-recruits. One such theft occurred about that time with disastrous consequences, involving the death from exposure of the owner who went in pursuit.

Among my various devices designed to secure the eggs and young of *Nautilus* I employed a tangle-drag, a bar of iron with long hempen tangles hanging from it, which was sunk in deep water in places frequented by *Nautilus* and left for a varying number of days with a buoy at the surface. I obtained the spawn of other Cephalopods by this means, but not that of *Nautilus*.

Another obvious method of dealing with this intractable creature was to bait and sink fish-baskets in the usual way, and to leave them down for several days instead of raising them at the customary time. This method was based upon the principle that, while it began to seem hopeless to think of acquiring the eggs in any other way than by inducing *Nautilus* to breed in confinement, it was not necessary to look at the captive specimens at once. In this way I sought to avoid the shock of bringing them to the surface before they could have a chance to settle down to the work of oviposition. Previous experience had led me to anticipate that the provisioning of the cages after the exhaustion of the bait would be accomplished automatically by the entrance of Crustacea and soft-shelled Echinids. *Nautilus* duly entered the traps, but in spite of sanguine hopes the experiment did not succeed, owing probably in part at least to various hindrances, such as the fragile construction of the cages, the inroads of conger-eels and the buffetings of other large fishes in the depths.

A further hostile element which has to be reckoned with when operating in deep water is the periodical visitation of gales of wind or half-gales, especially during the north-west season. These will often mercilessly dispel all one's hopes and contrivances.

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[1] Quoy et Gaimard, "Voyage de l'Astrolabe," *Zool.* T. III. 1834, p. 604. Atlas (Mollusques, etc.) Pl. 91, fig. 3. Dr Sluiter (Tunicaten in Semon's *Forschungsreisen*, Bd. V., 1895) has described this species under the name *Styela* (*Polycarpa*) *pneumonodes* and was the first to note the peculiar condition of the dorsal tubercle (cf. Sluiter, *op. cit.*, Atlas Taf. X. figs. 1—3).

[2] I procured more material with a small beam-trawl, which I took out with me from Plymouth at the recommendation of Mr J. T. Cunningham, than with the dredges, among my prizes being two very fine Polychaet worms belonging to the genera *Psammolyce* and *Palmyra*.

"Paraparau" and "malira" are local ordinances relating to marriage. The former, as I understand it, corresponds to a betrothal, but does not involve the appearance of the prospective bride. If a man is in a position to marry, he makes or observes "paraparau," going into retirement for a time, organising festivities and leaving the question of a bride to the last. It is defined by Mr Rickards, the author of the dictionary from which I have previously quoted, as the native custom of concealment during the preparation of marriage.

"Malira" is a term applied to substances employed as love-charms, and it also appears to be the more general name for a marriage festival or fair[1]. At all events towards the end of May (1895) a "malira" was held at Karavia close to my house. All through the night on the eve of the fair, natives were coming in from the bush, shouting at intervals in a loud monotone, blowing conchs and beating garamăts. When day came the company sang chants.

At a "malira" which I attended at a place called Pal-a-kulau (literally, house of cocoa-nuts) behind Karavia, the natives sang chants in a specially erected spirit-hut which was surmounted by feathers, rattles and coloured leaves and filled with carvings of human figures and birds. Scores of natives attended, marching in procession and carrying wooden effigies of pigeons suspended from long switches. One man came wearing a skull-mask ("a lor") made from the facial portion of a human skull plastered over with "tita," hair and beard being ingeniously glued on, in true semblance of humanity. The carvings were all on the flat except the pigeons. There was also a distribution of "bue" (betel-nuts) and diwara, but the latter was presented to certain people only. The food, contributed from different quarters, was wrapped up in banana leaves and was all paid for with diwara. The dancing, in which the women joined, consisted in circling round a "garamăt" and was accompanied by singing.

In illustration of the working of "malira" in its quality of love-philtre I may quote the following story which came to my knowledge. It seems that a man and woman who are "nimuna[2]" with one another cannot eat or even carry food in each other's presence, this abstention being a mark of respect. When a man desires to pay court to a woman he will lie in wait for her as she is walking through the bush and will then throw a "malira[3]" at her. If she knows who the man is through previous understanding and if she likes him, she will pick up the charm and put it in her basket. But if she intends to reject her suitor she will roundly abuse him and may lodge a complaint with her husband, who will promptly demand "tambu" from the offender. This is obviously a fruitful source of blackmail, and a case of the kind happened near Maulapao[4] shortly before I left New Britain, a man being accused by a woman who was his "nimuna." The woman stated that as she was walking through a patch of the long grass called kunè or kunai, which is used for thatching houses, she heard something rustle in the grass, but in searching for a "malira" was unable to find one. Whereupon with true native logic she made a long detour and finally found her victim hiding away with a couple of cocoa-nuts, as he knew his "nimuna" was passing through the neighbourhood and he could not let her see him with food in his hands. In consequence of the woman's assertions her husband demanded ten fathoms of diwara from the alleged offender although there was no proof whatever against him. If the woman heard anything at all in the grass it was most likely a lizard and she concocted her story on the strength of it. The last I heard of the affair was that the parties had submitted the matter to Mrs Parkinson's arbitration.

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[1] The women are soil-tillers as well as wives, and I think the "malira" is a kind of fair analogous to the old sessional fairs in the provincial towns of England where farm-labourers were hired.

[2] The term "nimuna" signifies the relationship between a man and his wife's parents and with those who are "tamana" with her (Rickards). "Tamana" is the relationship between father and offspring and between the latter and the father's brother.

[3] Consisting of a piece of bamboo or leaf with something wrapped up in it, perhaps some bark-scrapings from a particular tree with a little lime mixed in.

[4] The name of the site upon which Mr Parkinson's house stands.

In the course of my relations with my assistants I became acquainted with several of the minor traits of the native character.

Sometimes they fall ill and ascribe their malady to the influence of "puta." They are very careful to conceal or destroy all waste-products of their food, an admirable custom, but if they fail to do so by inadvertence, an enemy can collect the refuse and work mischief with it by sorcery. This branch of sorcery is called "puta" and one of my men, To-warabur, fell a victim to it, according to his own account.

When they see a log of wood or a bamboo-stem, floating vertically in the water and bobbing up and down, as often happens, they are frightened and filled with veneration for it, calling it "a tuk." On one occasion we passed such a drifting bamboo rod upon the top of which there were some accidental marks so disposed as to convey a grotesque resemblance to the human face. One of my boys, To-iraran, fled behind the mast in terror of this ill-omened taberan or demon. I then learnt that a former assistant of mine, a "koloata" or man of the bush, called To-bokat, who had fallen sick and returned to his village, had traced his affliction to the retribution due to him for having innocently hurled some stones at one of these vagrant logs.

Once I thought I had purchased the fidelity of two bearded men of Davaun but they disappeared during the night. I went to Davaun the next day to demand an explanation and was told that To-palavur's mother was sick and had said "very good they no go belong whity man." This affords an illustration of the working of the native idea of the "kubak," according to which the friends and relatives of a sick person who have slept within the same house or enclosure as the patient cannot spend a night elsewhere without causing a turn for the worse.

In the middle of July I left Karavia to take up my quarters in a recently vacated trader's house at Baravon on the other side of the bay, where there is good anchorage during the south-east season. I stayed here for some time, the chief objection to the place being that it was overrun by rats, which manifested the utmost impudence and indifference to the presence of a white man in their midst.

In August I paid a visit to the Credner Islands, called locally the Pigeon Islands, of which Nanuk is the smaller and Palakuvur the larger. These uninhabited islands are purely coral-formations, covered with vegetation, surrounded by reefs with a passage between the islands and a beach of white calcareous sand. On a subsequent occasion I procured here numbers of the interesting Enteropneust, *Ptychodera ruficollis*, but this time I accidentally incapacitated myself for serious work by biting into an uncooked taro. I had anchored on the reef at Nanuk for the night, it being high water, and intended to sleep on the boat while my boys lighted a fire and made themselves comfortable on the beach, cooking taro for themselves and for me. During the night it rained and thundered, and thinking to console myself with a taro I groped in the dark amongst the litter of ropes and gear, picked up one of these excellent fruits of the earth and made a lusty bite into it. It proved to be uncooked but I recovered from the dire effects within the twenty-four hours.

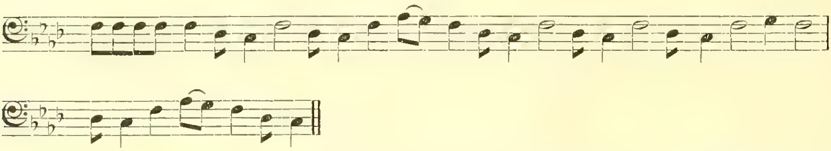
In the middle of August a note was brought to me from Mr Reuben Buckley, a trader quartered in the Malagunan district quite at the other end of Blanche Bay, saying that *Nautilus* was also found off the north coast of the Gazelle Peninsula. Accordingly the next day I paddled over to Malagunan and was conducted overland to a place called Matakabang on the north coast, the road between these two villages being flanked on the east by the heights of the North Daughter. From Matakabang we pulled across to a district at the head of Talili Bay called Unakămkămbi, where there was another trading station tenanted by Mr MacNicoll. Here I made arrangements for traps to be set for *Nautilus* and next day returned to Blanche Bay to raise up some coral blocks which I had previously sunk in a selected spot in about 80 fathoms. On examining the coral trees I found numbers of the large Ostracod crustacean which has been described by Mr Stebbing under the name *Asterope arthuri*, but no signs of *Nautilus*.

The next morning I set sail for Unakămkămbi, rounding Praed Point and Cape Stephens. I spent the best part of a month at this place, having found the conditions for pursuing my search for the young of *Nautilus* almost as favourable in the south-east season in Talili Bay as they were in Blanche Bay, but not more so; in the north-west season I think it would be impossible to operate in Talili Bay. Near the eastern limit of Talili Bay there was a Catholic Mission station, administered by Père Bley, and at the western point a Wesleyan Mission station, presided over by Rev. J. A. Crump, at the village of Kabakada adjoining Unakămkămbi.

I have made occasional reference to certain New Britain usages according as I had opportunity to observe or to take part in them, and it is impossible to leave this island without a word concerning two of its most characteristic and well-known institutions, the Dukduk and the Tubuan. They are cognate organisations ordained for the glorification of departed chiefs and to promote the circulation of diwara, although this brief statement does not exhaust the sum of their functions. It appears that the Tubuan is supposed to die periodically and to be born again. I once witnessed a most interesting representation of the resurrection of the Tubuan, which took place opposite to my house at Barawon near the village ruled over by an important chief named To-kinkin.

At midnight, in the month of July (1895) a couple of Tubuans from Matupi, escorted by a fleet of forty or fifty canoes, arrived at To-kinkin's place. They had brought with them a carved human emblem representing a personage whom they called To-ririg, doubtless a great man of former days. This circumstance suggested to me the possibility of the dukduk and its subsidiary tubuan being a means by which the history of the tribe is handed down from one generation to another[1]. Throughout the rest of the night the natives uttered awe-inspiring howls at frequent intervals. After sunrise they took to their canoes again, the two Tubuans in separate canoes, and the entire flotilla pulled out to the middle of the bay, where they came to rest. The Tubuans thereupon executed an elegant dance with due restraint in their respective canoes, apparently illustrating their regeneration from the sea in the manner of Aphrodite[2]. The setting for the performance provided by the natural features of the bay was most picturesque and impressive, and the effect was heightened by the chant which was intoned by the assistants.

Tubuan Chant.



The more important Dukduk is dressed like the Tubuan in the bird-costume, the chief difference being that the conical head-dress of the former is much longer than that worn by the Tubuan. The Dukduk observance may be a very elaborate ceremony[3], but for my part I saw some dukduks on the beach at Matupi on one occasion only. I was informed that they had been engaged by an old chief who expected to die but recovered.

On several other occasions while I was in New Britain a Tubuan was to be seen dancing along the beach skirting Blanche Bay, shouting to scare the women. Sometimes the Tubuans are engaged instead of the Dukduks, I think on account of the smaller expense, to celebrate the funeral rites of a deceased chief. None were present at the only native funeral which I attended, but another funeral was taking place elsewhere at the same time, at which two Tubuans were employed.

If the seven principal features of New Britain life which I have briefly touched upon be enumerated in the following order, pepe, maravot, igiat, paraparau, malira, tubuan, dukduk, we shall gain I think a fairly accurate insight into the sequence of ceremonial observances in this wonderful island.

Towards the end of September (1895) the "Ivanhoe," a topsail schooner of 152 tons, Capt. James Steele, unexpectedly arrived at Herbertshöhe from British New Guinea on a trading cruise. She was to return to Cooktown by way of New Guinea and after long consideration I determined to continue my quest in the neighbourhood of Milne Bay, knowing well the importance of keeping on the move while engaged in such work as that to which I was committed. I took leave of my kind friends at Ralum with many expressions of regret and sailed away on board the "Ivanhoe" on October 12th. With a fair wind we should have reached Samarai or Dinner Island, the headquarters of the Government in the Eastern Division of British New Guinea, within four days, but contrary winds, squalls and calms delayed our arrival until October 25th. Here I lost no time in procuring a small decked cutter, the "Mizpah," which at once provided me with shelter and means of conveyance, although I was not so much in need of the latter, having brought my boat from New Britain. But the need of sleeping accommodation decided me to acquire the "Mizpah" and, on the whole, I had no reason to regret the purchase.

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[1] Compare Graf von Pfeil, "The Duk Duk and other customs as forms of expression of the intellectual life of the Melanesians." *Rep. Brit. Ass.*, 1896 (Liverpool), p. 939.

[2] The costume of the Tubuan, consisting of a tall conical mask topped by a plume of white feathers and passing below into a heavy stack of leaves reaching from the shoulders to the knees, is intended to represent the figure of a bird, and what is known of bird-symbolism may suffice to justify the above comparison, although I have no actual information on the subject.

[3] Cf. Meyer, A. B., and Parkinson, R., *Album der Papua-Typen*, 1894. Pls. 13 and 16.

The shells of *Nautilus* are found in great numbers among the islands which compose the eastern archipelago of New Guinea, and it was this information which induced me to ascertain whether there might be any prospect of meeting with a more suitable locality in these waters. It is a curious reflection that although *Nautilus* ranges over a large part of the Indo-Pacific Ocean from the Philippines to the Fijis, at no point within the sphere of British influence[1] is it available for practical investigation. Stray specimens may be caught here and there but it is only to the Philippines, Moluccas, Bismarck Archipelago or Loyalty Islands that we may look for the final solution of the mystery surrounding the propagation of *Nautilus*.

The natives of the country round Milne Bay and of the neighbouring islands are not great fishermen and do not make elaborate fish-baskets, so that they contrast very noticeably in this matter with the men of New Britain. Perhaps the reason for this may be that animal food is more plentiful in the bush in New Guinea than in New Britain, where pork may not be eaten by members of the tribal fraternity of the igiat. Whatever the explanation may be, the fact remains that while the natives may be seen fishing with a seine on the reefs, they neither employ the larger traps nor do they know how to make them.

I commenced operations in the D'Entrecasteaux Group, putting up a temporary house on an uninhabited coral islet called Karuana, close to the important island of Sanaroa[2]. This was a delightful spot and a capital site for a biological station, as the surrounding seas contain numerous coral-patches.

I explored Hygeia Bay on the coast of Fergusson Island. On this island the natives were rather a wild-looking lot, such of them as came down to the beach. They carried cosmetics and charms in bamboo[3] tubes, and some of them wore head-ornaments or chaplets consisting of a fringe of yellow feathers (from the crest of the cockatoo) rising from a border of red parrot feathers, closely resembling a similar ornament used by some Indians of the Amazons region.

I put down a basket here but the resulting captures of a small viviparous shark, crustacea, etc. offered little encouragement for *Nautilus*. There is an extensive reef at the north-west corner of the bay and good anchorage on a sandy bottom at the south-west corner where there is also a deep freshwater creek not marked on my charts. I took three soundings across the mouth of Hygeia Bay in a northerly direction showing 59 and 66 fathoms of water, but at the third sounding the line was bitten across, probably by a hungry shark, and the lead was lost.

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[1] With the possible exception of the Fiji Islands from whence, so far as I know, no preserved specimens have been sent either to Australia or to Europe, in spite of the existence of circumstantial accounts of the methods employed by the natives to catch them.

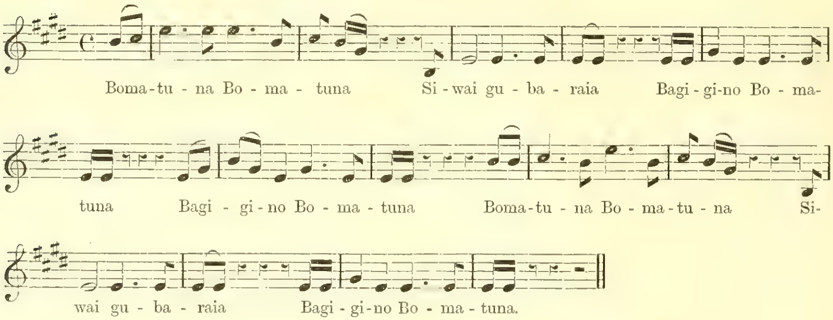
[2] Welle Island on the Charts.

[3] Bamboos do not occur in all parts of New Guinea and its dependencies, and those which grow on Fergusson Island are a feeble variety in comparison with the bamboos of New Britain and elsewhere.

Having injured my foot on the coral at Karuana my principal boatman, Suopa, made me a poultice by scraping some raw yam with a shell and cooking it in a frying-pan; he told me to put a little sugar in it and apply it to the foot. I did so and I think it undoubtedly assisted the inflammation and reduced the pain.

Frequently my boys would break out into song and sometimes with their clear natural voices the effect produced was quite charming. Once when I was busy in my cabin my skipper started a spontaneous anthem in honour of the south-east wind ("bomatu") and was soon joined by the little cook in unison.

Hymn to the south-east wind.


Boma-tu - na Bo - ma - tuna
Si - wai gu - ba - raia
Bagi - gi-no Bo - ma-
tuna
Bagi - gi - no Bo - ma - tuna
Boma-tu - na Bo - ma-tu - na
Si-
wai gu - ba - raia
Bagi - gi-no Bo - ma - tuna.

Among the reef-patches at Karuana I made the acquaintance of a remarkable species of fish, the *Amphisile strigata*[1] of Dr Günther. This species lives in small shoals of about half-a-dozen individuals and swims about with rapidity in a vertical position, cleaving the water with its razor-shaped body. I was greatly astonished when I saw these spectral fishes flitting about and I pursued them with much perseverance in my dinghy, but although I came up with them several times they doubled back with such deftness that they completely baffled my attempts to catch them with a pole-net. Subsequently I obtained specimens at Lifu in which I recognised my Karuana friends. The tiny mouth is placed at the summit of the pointed snout and is only capable of imbibing microscopic nourishment.

At the eastern extremity of the mainland of New Guinea there is the famous inlet of Milne Bay, at the sight of which I was tempted to believe that all things were possible in its untried depths, but so far as *Nautilus* is concerned I met with no better fortune here, after trapping and trawling for a fortnight, than in Hygeia

[1] Kindly identified by Mr G. A. Boulenger, F.R.S., from specimens taken at Lifu.

Bay. It is true that a single specimen of *Nautilus umbilicatus* was picked up from the surface of the neighbouring sea and reached my hands later in a mangled condition. From this circumstance it would seem possible that systematic search on an extensive scale with unlimited equipment would discover a *Nautilus* ground in New Guinea waters. But from all I can hear, it is likely that the Philippine Islands will prove to be the vantage ground for this investigation[1].

An old pearler whom I met in Milne Bay on board his cutter informed me that he did not think *Nautilus* lives in Milne Bay, but the shell drifts into the bay from the windward from such places as Teste Island, Brooker Island and the Du Chateau Islands[2], although some natives said they had taken it in the bay long ago.

Shortly after leaving Milne Bay I was sorry to lose the services of my native skipper, Suopa, who was a cheery fellow as well as a handy man. Knowing that it was my ultimate intention to leave New Guinea in order to seek out some more likely place, he one day offered to follow me wherever the four winds might take me, not caring even if it should so fall out that he never returned home. I was rather touched by this assurance of devotion, the more so because I knew that it would be contrary to regulations to accept his offer of service away from New Guinea, but I was quite unprepared for the reaction which set in the very next day when he demanded money and freedom, and, not content with these, began raking up old scores as a reason for leaving.

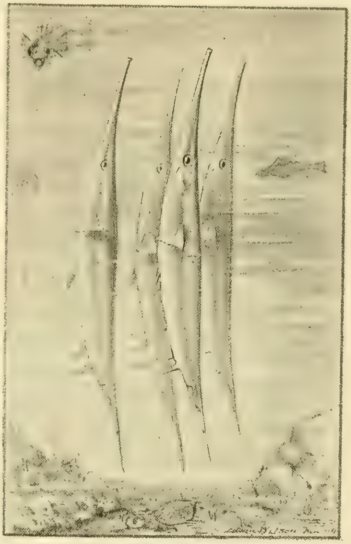


FIG. 12. Shoal of *Amphisile strigata* in attitude of swimming. They are represented as if swimming from right to left. (Drawn by Mr Edwin Wilson.)

Next day I sailed east, in the direction of the Conflict Group, with a crew of three mop-headed youths, including a little fellow whom we called "Cookie," but whose real name was Taliwanedi, a native of Sanaroa.

The distances between the numerous groups of islands into which the eastern division of Papua is subdivided, are not very great, but the opposing winds, currents and calms render navigation uncertain and sometimes precarious even to a seasoned mariner.

On the 14th of January, while nearly becalmed and drifting within sight of the low-lying western islets of the Conflict Group, a shell of *Sepia*, often called the cuttlebone, came floating by, borne along by a two-or-three-knot current to the north. One of my boys who knew my interest in flotsam, jumped into the dinghy with praiseworthy dispatch and secured the shell.

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[1] Cf. Dean, Bashford, "Notes on Living *Nautilus*." *Amer. Natural.* xxxv. pp. 819—837, 1901.

[2] I had intended to visit these islands, but the imminence of the south-west monsoon in this region prevented me from getting farther east than the Deboyne Group, except at a risk of being wind-bound.

It had been afloat long enough to allow many kinds of larvae (Crustacean, Anthozoan, Annelid) to attach themselves to it whether as a temporary resting-place or as a permanent foundation. I placed it in an enamelled basin with sea-water, whereupon many of the organisms detached themselves and swam about in the dish. My attention was soon attracted by some small flattened disc-shaped bodies about one-third of an inch in diameter which could both creep and swim. As they crawled along they jerked out a pair of milk-white tentacles having a worm-like motion of their own, and quickly retracted them, repeating the process continually. My joy was complete when I recognized in these small creatures the very remarkable genus *Ctenoplana* of which only one specimen had ever been seen before, namely in 1886 by Prof. Korotneff, who found it in the plankton or drift-fauna off the coast of Sumatra.

Although cramped for space in the little cabin of my cutter I had the necessary appliances for making a cursory examination of anything which required immediate attention and was thus able to make some additions and emendations to the account furnished by the original discoverer, and I considered that my re-discovery of *Ctenoplana* made amends for a great deal of trouble and disappointment.

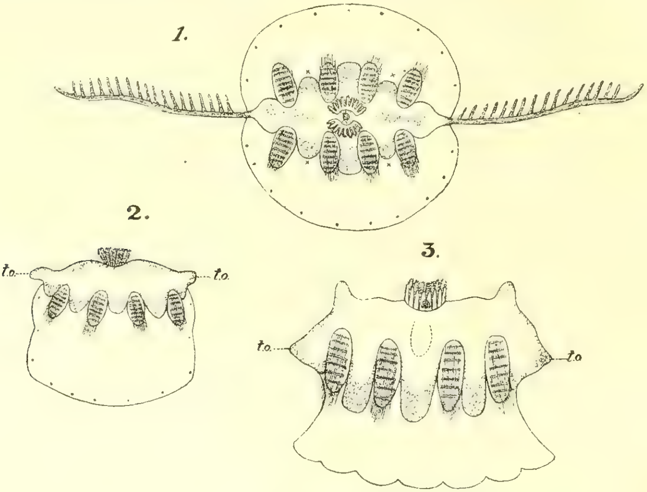

Fig. 13. *Ctenoplana*; (1) from above in attitude of creeping with tentacles extruded; (2) and (3) side-views in attitude of swimming. The first two are the red form, the third is the green variety which contained male gonads; *t.o.* position of orifice of the sheaths of the pinnate tentacles. (After Willey, *Quart. J. Micr. Sc.*)

Ctenoplana is one of those puzzling creatures which rack the brain of the controversial morphologist in his futile effort to arrive at a provisional settlement of a point in phylogeny. When it is creeping along the bottom of a dish or, back downwards, along the surface film of water, it looks for all the world like a Polyclade Turbellarian. The fitful extrusion of the opaque white tentacles which have serpentine intrinsic movements of their own, reminds one involuntarily of the behaviour of the Nemertine with its proboscis. On the other hand, when *Ctenoplana* undertakes to swim, it does not do so by the graceful skirt-like evolutions of the Polyclade, but it assumes a helmet or Pilidium shape, depressing the two halves of the body until they assume a vertical position like the flaps of a bonnet, and then a set of organs, called ctenophoral plates, which are utterly foreign to Turbellarians but distinctive of a group of hyaline pelagic organisms, the Ctenophora, come into play.

The ctenophoral plates which, as I have said, are the swimming organs of *Ctenoplana*, occur as eight small oval areas on the dorsal surface. Each plate is beset with a limited number of transverse rows of powerful cilia agglutinated together at their bases so as to form a membrane upon which the cilia are inserted like the teeth into the back of a comb.

These characters seem to indicate that *Ctenoplana* occupies a central position midway between the pelagic Ctenophora and the littoral Plathelminthes. This, however, is the simple view of the matter and there are many practical obstacles to its adoption. Some zoologists contend that *Ctenoplana* is to be interpreted as a specially adapted creeping Ctenophore, but as a result of my observations, which unfortunately left many questions still unanswered, I advocated its ordinal autonomy, chiefly on the ground of its possession of distinct male genital ducts opening to the exterior on the dorsal surface of the body[1].

The principal features of interest in the organisation of *Ctenoplana*, features which cannot fail to mark it out for special discussion whenever the interrelations of the lower orders happen to be adjudicated, may be summarised as follows:—

I. Abstract positive features.

a. Dorsiventral differentiation.

b. Biradial symmetry.

c. Main axis passing between the median ventral mouth and the median dorsal sensory apparatus.

II. Abstract negative features (involved in the preceding but worthy of special tabulation).

a. Absence of antero-posterior differentiation.

b. Absence of ambidextral differentiation (there is no right and left).

III. Concrete positive features.

a. Ctenophoral plates.

b. Semi-opaque, pigmented integument.

c. Paired pinnate tentacles (Greiftentakeln).

d. Paired aboral, ciliated, sensory papillae.

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[1] Willey, A., "On Ctenoplana." *Quart. J. Micr. Sc.*, Vol. xxxix., 1897, pp. 323—342. Pl. 21.

e. Ciliated ectoderm on ventral surface.

f. Male gonads with tunica propria.

g. Male genital ducts opening to the exterior on the dorsal surface.

The fact of biradial symmetry means, of course, that there are two planes of symmetry which divide the body respectively into two equal halves. One of these planes passes through the muscular pinnate tentacles, and is called the tentacular plane of *Ctenoplana* and of the Ctenophora generally. The other plane cuts the tentacular plane at right angles, and corresponds to the so-called stomachal or gastral plane of the Ctenophora. Corresponding with these two planes we have the two axes, namely, the *tentacular axis* and the *gastral axis*.

Armed with a few new facts, one is strangely tempted to enter the lists of biological speculation and take one's chance in the *mêlée*, or in other words, to make some addition to the discussion concerning the relation of the above-named planes and axes of biradially symmetrical animals to the planes and axes of bilaterally symmetrical animals such as Turbellarians and Annelids. The chief question which fixes the attention of the observer is this:—Is it the tentacular plane or the gastral plane which is homologous with the sagittal plane of a bilateral worm? or, to put it more brusquely, Is it the tentacular axis or the gastral axis which corresponds with the oro-anal axis of a Nemertine or an Annelid?

It might be and I believe it has been contended that there is no ground for comparison between the axes of a Ctenophore and those of a worm, in which case the question propounded above has no point. Freely admitting that this may be true, there is still room to suppose that it may not be true. Assuming therefore that one or other of the biradial planes must represent the sagittal plane of higher forms, I give it as my own conviction that the tentacular plane of *Ctenoplana* about which the aboral ciliated sensory papillae are disposed in paired groups as shown in Fig. 13, coincides with the sagittal plane of a bilateral Turbellarian, Nemertine, or Annelid.

Much as the prominent pinnate tentacles of *Ctenoplana*[1] simulate transversely-paired organs, they are not more paired than are the ciliated sensory tentacles of the same animal. Both these organic systems, however, are paired about different planes and it is to this circumstance that the discussion which I have outlined is due. I simply desire to emphasize what I believe to be theoretically sound, namely, that if the above-named planes are held to be respectively comparable, then the tentacular plane of *Ctenoplana* and of the Ctenophores[2] represents the sagittal plane and the pinnate tentacles occur in this plane, like the proboscis of the Nemertines. Either there is no correspondence at all or the tentacular and sagittal planes are homologous, but to my mind there can be no question of the gastral axis of *Ctenoplana* corresponding with the antero-posterior or oro-anal axis of the bilateral forms.

Whatever the truth may be, *Ctenoplana* remains a remarkably interesting type and no zoologist could encounter specimens of it without experiencing a momentary thrill of satisfaction. Of the four specimens which I obtained three were mottled with green, the fourth with red pigment; the former were rather larger than the red variety and differed from it somewhat in shape. The red form also differed in minor details from the original type *Ctenoplana kowalevskii* Korotneff. Nevertheless, with added experience of specific divergencies, I am now inclined to think that my *Ctenoplana rosacea* is co-specific with Korotneff's type, and it seems quite likely that the green form is nothing more than a variety or phase of the same species.

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[1] The same applies to the Ctenophora in a less obvious sense. For discussion of the axes of Ctenophora the reader should consult Prof. Chun's Monograph, *Die Ctenophoren des Golfes von Neapel*, 1880.

[2] This is the view, as concerning the Ctenophora, which was first held by Professor Chun, but he seems to have made a subsequent retractation.

All the green individuals contained male gonads with their genital ducts, but I was unfortunately unable to satisfy myself concerning the female gonads. It should be noted that great care and the application of very special methods are requisite for the preservation of *Ctenoplana*. It is well known that some of the Ctenophora dissolve away before one's eyes in certain fluids, and although *Ctenoplana* does not vanish in this way, the contraction of the tentacular musculature is apt, in healthy specimens, to cause a lamentable shrinkage.

In his recent account of the Ctenophora[1] Mr G. C. Bourne places *Ctenoplana* and the allied genus *Coeloplana* in a special order of Ctenophora Tentaculata, which he names *Platyctenea*, at the same time declining "to attach very much importance to the resemblance between *Ctenoplana* and the Polyclada." Mr Bourne further comes to the conclusion "that the Turbellaria, the Nemertines and the Ctenophora are descended from a common ancestor which is most nearly represented by the larva of *Stylochus*" [a Polyclade worm]. This is mainly in accordance with the views which I expressed in my paper, and Mr Bourne quotes the *Pilidium* larva of Nemertines in his comparison, as I also did. Moreover, the term *Platyctenea* is undoubtedly preferable to the term which I suggested, *Archiplanoidea*, as an ordinal name, but I am unwilling to refuse any importance to the latter name. I intend it to embody the proposition originally laid down in its main principles by Prof. Chun, that the bilateral Plathelminthes generally have originated from a biradially symmetrical ancestor, and further to express the possibility of the diphyletic origin of triploblastic animals.

After much labour against the tide we managed to get to a temporary anchorage off the westerly islet of the Conflict Group, intending to make the lagoon before dark, but failing to find the passage we spent a squally night tacking about. Towards the evening a remarkable procession of transparent pelagic animals, Ctenophora of several different kinds, including the ribbon-shaped *Cestus*, drifted past the islet. These creatures, as I have said, are most difficult to preserve, as they have the peculiar property of undergoing instantaneous disintegration and dissolution under certain conditions of treatment.

Next morning I had quite lost my bearings and suddenly found myself heading straight for the reef, but I got the jib and sail down just in time to avoid a collision. It was not until the following sundown that we found the passage and anchored in the lagoon. Just about this time the south-west wind began to blow and I found the lagoon with its loose sandy bottom a most uncomfortable anchorage. In this region the two predominant winds are the south-east and the south-west monsoons, the latter corresponding with the inclement season which in fact begins to set in towards the end of January. The numerous islets surrounding the Conflict Lagoon, which is upwards of 20 miles in length, are uninhabited, the natives merely using this as a half-way house on their long canoe voyages. At the time of my visit, as I have said, the south-west squalls commenced and, increasing in severity, my two anchors persisted in dragging, so that on the fifth day there was no other course open to us than to get clear of the lagoon which had become a veritable trap, if we wished to avoid the ignominious piling up of our craft on the reef. After being foiled in several attempts we emerged successfully through a narrow passage nearly opposite to the one by which we had entered the lagoon. I think it must have been blowing quite half-a-gale and the sea was running high, but the Mizpah's thin boards held together and we spent the night tacking and drifting in the usual manner. On the following day although the wind had moderated I had again lost my bearings and was at my wits' end to know which course to set in this reef-bound sea, when we espied another cutter two or three miles ahead and decided to follow her lead. In due course our unconscious pilot disappeared through a passage in a distant reef and I headed straight for this point to the best of my belief, but on arrival was confronted by a continuous reef which seemed to stretch on either hand as far as the eye could reach from the mast-head. By following up the reef, though labouring under total misapprehension as to the identity of the various islands around us, we suddenly found ourselves in a wide passage which, as we subsequently ascertained, led us into the magnificent lagoon of the Deboyne Group, at the northern end of which stands the high crescentic island of Panaieti, overshadowed by the loftier crest of Misima to the north-east.

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[1] *A Treatise on Zoology*, edited by E. Ray Lankester, Part II. chap. VII. 1900. The Ctenophora by G. C. Bourne, M.A.

Inside the Deboyne Lagoon there is another hilly island called Panapompom, off which we anchored and set about purchasing food, our stores having run out, but only bread-fruit was procurable. The natives of Panaieti are in the habit of crossing over to the south-east side of Panapompom in order to cultivate gardens of yams, sweet-potatoes, pumpkins and bananas, which however do not form a conspicuous feature in the scenery as they do in the Engineer Group and other more westerly islands.

While at anchor in the lagoon I put down a small dredge, taking it out in the dinghy for some distance, then sinking it and hauling in with the hand-winch on board the cutter. I was rewarded for my pains by finding in the sand with which the dredge became filled a species of lancelet (*Amphioxus*) belonging to the genus *Asymmetron*, which had only been discovered a few years previously by Prof. E. A. Andrews[1] at Bimini in the Bahamas.

The family of the Branchiostomidae, which includes all the known species of the lancelet, occupies such a peculiarly central position in the system of animal life, and its distribution is so local, that it is always satisfactory to ascertain a new fact concerning either its organisation or its range[2]. I was not a little surprised to find a representative of this West Indian species in the Louisiade Archipelago and subsequently in Sandal Bay, Lifu, although it is a fact that there is a strong Caribbean element in the fauna of the Indo-Pacific. Still it is interesting in consideration of the fact that two other species of the same family belonging to different genera, *Amphioxus belcheri* and *Epigonichthys cultellus,* occur in Torres Strait and the Moluccan Sea but have not been found in the West Indies.

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[1] Andrews, E. A., "An Undescribed Acraniate: *Asymmetron lucayanum*." *Stud. Johns Hopkins Univ.*, v., pp. 213—247, 1893.

[2] Willey, A., "Zoological Observations in the South Pacific." *Quart. J. Micr. Sc.*, Vol. 39, p. 219, 1897. *Amphioxus belcheri* has its southern limit in Moreton Bay, Queensland, and its northern in Japan. It has been

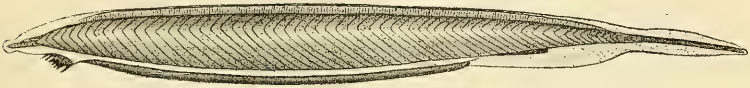

FIG. 14. *Asymmetron caudatum* (probably a sub-species of *A. lucayanum*). A number of the oral cirri are united together by an intertentacular membrane; the notochord is continued as a urostyle behind the muscle-segments. Magnified about 7 times.

At the time of my visit, as I was informed by the resident Wesleyan missionary, the Rev. Ambrose Fletcher, the population of Panaieti numbered 466 men, women, and children, who live in a series of villages on the south side of the island facing the lagoon. The island is rocky and the soil unproductive, so that food is often scarce. The natives, however, are great sailors and canoe-builders and cover long distances by means of their huge mat-sails. More than half the population may be absent from the island during the south-west season, in search of food, pigs, yams and so forth. The houses are well built and have a characteristic shape, somewhat resembling a huge inverted whale-boat, often with a verandah-like platform in front. In every village there was a small bar of wood supported upon a couple of uprights and bearing numerous lower jaws of pigs to show what the natives had eaten, the skeletons of former feasts which could be contemplated in times of stress. The uprights were often surmounted by a cocoa-nut, reminding me that in New Britain the husks of cocoa-nuts were wont to be displayed in a similar manner. It would appear that these people exist largely upon the "bare imagination of a feast," and at this time of the year (January) food was very scarce, bread-fruit and nuts called "siaia" being the chief commodities, while hunger can always be staved off by chewing the areca nuts which they obtain from Misima. The "siaia" nuts are roasted in the fire or cooked in clay-pots and have an agreeable taste. Another species of nuts called "dausia" has to be soaked for five days in sea-water either before or after being cooked, in order to remove its noxious properties and render it edible.

The piles upon which the houses of the Panaietians are raised, are fitted with large circular wooden discs perforated in the centre to admit the post; they are called "panapana" and are intended to prevent the incursions of rats into the dwellings.

Tattooing is not practised at Panaieti, but the teeth of the women are blackened and the ears pierced upon arriving at puberty. Should a young girl join the mission, the old women of her village will urge her to leave the white man ("dimdim"),

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recorded from Singapore by the late Mr Bedford. The lancelet of the Bass Strait (*Heteropleuron bassanum*), as I ascertained from specimens in the Australian Museum, Sydney, kindly shown to me by Mr Thomas Whitelegge, ranges north as far as Port Jackson.

saying, "Your teeth are not blackened and your ears are not pierced, no man will marry you."

After having been kindly entertained by Mr Fletcher, who insisted upon my acceptance of a supply of coffee and tea, I started to leave Panaieti shortly after sunrise on January 30th, with a light wind. Towards noon a northerly breeze carried us through the passage between the Torlesse Islands and the Panaieti reef. There was a lively tidal rip in the passage, and just as we emerged from it the wind ceased and the tide turned simultaneously, as so often happens, and we drifted back into the lagoon, where in the pale moonlight we soon found ourselves scraping the surface of a submerged reef. I did not know where the next tack would bring us, but it happened that a welcome land-breeze came to our assistance, enabling us to make the passage once more during the night, and a couple of days later we reached the island of Tubetube in the Engineer Group.

The population of the Engineer Group was distributed as follows, Tubetube 350, Kuriva 260, Naruaruari 120. The natives are famous sailors and tillers, but poor fishermen. When mourning for relatives the women blacken their bodies, wear long leaf petticoats reaching nearly to the ground, a mass of cords round the neck and a necklace called "kokoana" of the large shells of *Ovulum ovum* ("dunari"). Only the women are tattooed all over the chest and abdomen and often upon the face as well.

The large canoes of Tubetube are made at the Woodlark Islands (Murua) and are decorated with bird scrolls at the ends and fish-representations on the hull. Wooden bowls in use here are also made at Murua, but the wooden scoops for baling out the large canoes are manufactured at Tubetube as well as at Murua. The clay bowls of Tubetube constitute a staple article of trade with other islands, more especially with Dobu; they are extensively moulded by women on the three islands of the Engineer Group, being shaped by hand without the aid of pottery whorls, by superposing circular bands of clay; of course they remain unglazed.

After another flying visit to Dobu and Karuana, where I had built a pile-dwelling on a former occasion, I returned to Samarai, from whence I made a voyage (accompanied by Mr C. H. Walker, with whom I stayed for a few days at Matadona on the western side of the China Straits) to the island of Suau, which forms the south cape of New Guinea. In several villages along the south-east coast I noted isolated instances of the round discs fitted on to the pillars of the houses as at Panaieti. I was told that there is a story current of the Savaiians (inhabitants of Savaia, a large village on the mainland not far from Suau, situated at the head of a bay, across the mouth of which stretches a formidable barrier reef) having fitted out an expedition to fight the Panaietians some years previously.

By this time I had become convinced that it would be useless to spend more time in searching the coasts and islands of New Guinea for *Nautilus*, in spite of the frequency with which the shells are cast upon the reefs. I therefore decided to go still farther east, either to New Caledonia, Fiji, or the New Hebrides, in any case by way of Sydney.

I spent my last somewhat fever-stricken fortnight in New Guinea under the hospitable roof of the Rev. C. W. Abel, of the London Missionary Society, on the small

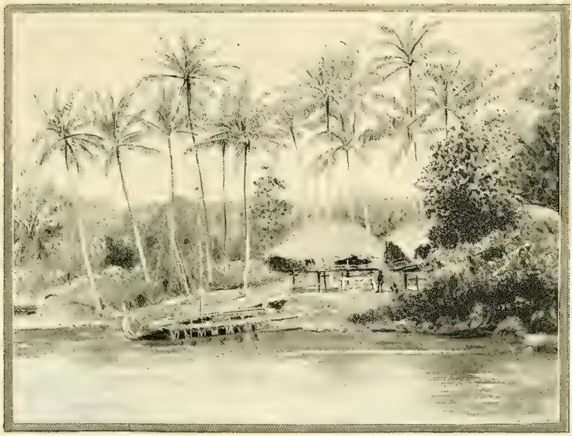

Fig. 15. Shore-scene at Panaieti showing pile-dwellings with rat-guards on the posts; a canoe is hauled up on the beach.

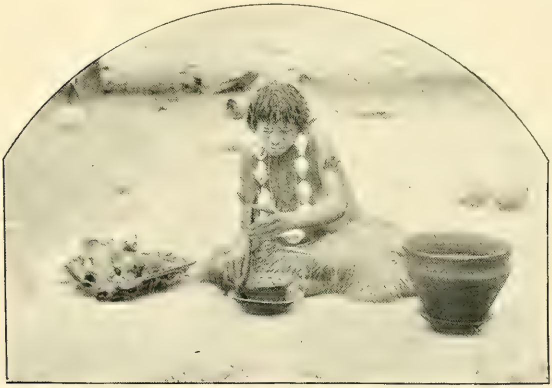

Fig. 16. A potter at work on the island of Tubetube; she is wearing a necklace of the shells of Ovulum ovum.

To face page 726.

island of Kwato opposite to Rogeia, within easy distance of Samarai, and left on board the S.S. Titus on March 28th, bound for Sydney by way of Sudest and the Solomon Islands, the full enjoyment of this interesting voyage being marred by intermittent attacks of fever.

We passed Sydney Heads and entered Port Jackson on April 20, 1896. I spent upwards of two months at Sydney, where I was accorded working space in the Biological Laboratory of the University by Professor W. A. Haswell, F.R.S., and was thus able to examine some of the material which I had collected, every facility and kindness being showered upon me by Professor Haswell and by my friend Dr J. P. Hill. I was also made free of the excellent library of the Linnaean Society of New South Wales, by the courtesy of Mr J. J. Fletcher, M.A., and received valuable information from the Director of the Australian Museum, Mr R. Etheridge Jr. and from Mr Charles Hedley and Mr Thomas Whitelegge. I learnt from Mr Hedley that *Nautilus macromphalus* was definitely known as the "Isle of Pines *Nautilus*" and this practically decided me to wend my way to New Caledonia. I therefore left Sydney on July 2, on board the Messageries Maritimes S.S. Tanais bound for Nouméa, making the passage through the marvellous barrier reef of New Caledonia on the fourth day out from Sydney. As some days must elapse before I could secure a passage to the Isle of Pines I made arrangements through the instrumentality of gentlemen to whom I had brought introductions from Sydney to accompany the Breton pilot, M. Le Ravallec, in the pilot-cutter to the lighthouse on the Ile Amédée, about twelve miles out from Nouméa, where the pilots await the arrival of steamers.

On the shore of Amédée I obtained my first specimens of a remarkable species of Enteropneusta, *Ptychodera flava,* which I afterwards found more plentifully at the Isle of Pines and also on the weatherside of Lifu, that is, on the side opposite to that on which Sandal Bay is situated. From the point of view of my own experience the observation of this species in the living condition, subsequently enhanced by the study of its organisation, threw a flood of light upon the structure of this group of burrowing "worms," which respire by means of gill-clefts, and it seemed to me that *Pt. flava* should be regarded as the type of the Enteropneusta from a morphological standpoint as it actually is upon chronological grounds, an opinion to which subsequent examination lent additional support.

It is a remarkable feature of morphological inquiry that one worker should find so many points of comparison between distantly related groups where another, often a very eminent authority, sees nothing of the kind; others again engaged upon similar investigations but starting with different premises ignore utterly the existence of groups of animals which seem to bear upon the matter. For example, I am ready to affirm with considerable confidence that the unpaired hollowed "roots" which pass between the medullary canal of the collar region and the epidermis, where they join the intra-epidermal fibrillar plexus in *Ptychodera flava* and in allied species, belong to the same category, in other words, are homologous with the pineal outgrowths of the primary fore-brain of Vertebrata. This is a conclusion which may possibly be supported by further observations, but can hardly be submitted to the test of experiment, and must therefore ever fail to convince the rightly sceptical.

The diagrams here reproduced are founded primarily upon conditions prevailing in the larva of *Amphioxus,* which are of the utmost complication as soon as one approaches them in a morphological spirit. In the Prochordata (including for the present occasion the Enteropneusta, Tunicata, and Cephalochorda) the three principal *canal* systems of the body, namely, coelomic, neural, and alimentary, open in various ways to the exterior in the anterior region, where they form an intricate association of apertures which I have formally designated as the *anterior trematic complex.*

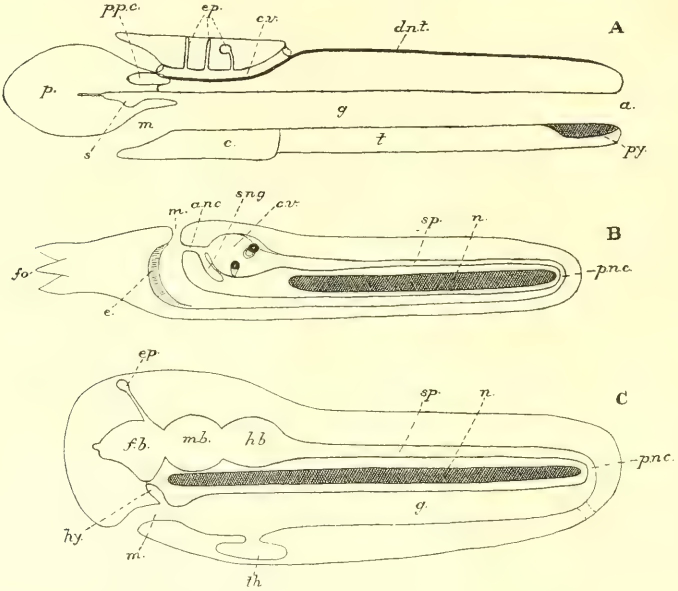

FIG. 17. Diagrams to elucidate some suggested comparisons between an Enteropneust (A), an Ascidian larva (B), and a Craniate embryo (C).

A. *p.* proboscis; *p.p.c.* proboscis pore-canal opening close to the anterior neuropore which leads into *c.v.* the collar nerve-tube; *e.p.* epiphysial roots; *s.* stomochord; *m.* mouth; *c.* collar-region; *g.* gut; *t.* trunk-region; *d.n.t.* dorsal nerve-tract; *a.* anus; *py.* pygochord.

B. *f.o.* organ of fixation; *e.* endostyle; *m.* mouth; *a.n.c.* anterior neurenteric canal which, together with *s.n.g.*, subneural gland, constitutes the neuro-hypophysis; *c.v.* cerebral vesicle; *sp.* medullary tube communicating with the gut by means of *p.n.c.* posterior neurenteric canal; *n.* notochord.

C. *ep.* pineal body or epiphysis cerebri; *f.b.* *m.b.* and *h.b.* fore-, mid-, and hind-brain; *hy.* hypophysis cerebri; *th.* thyroid gland; other letters as above.

The following table will possibly be useful to future investigators who may venture to wrestle with this problem.

Tabulation of structures concerned in the formation of the anterior trematic complex of the Prochordata, consisting of organs which are probably homogenetic and of their connections which are presumably related through metaleptic succession or substitution.

I. ENTEROPNEUSTA.	II. TUNICATA.	III. CEPHALOCHORDA.
Proboscis with a *head-cavity* or proboscis coelom communicating by a *coelomic orifice* with the proboscis *pore-canal* (or end-vesicle) which opens externally by the *proboscis-pore* in the vicinity of the anterior *neuropore.*	**Organ of fixation** with a *cavity* in which mesenchyme-cells circulate; probably a degenerate coelomic cavity but neither blastocoel nor haemocoel; it is a deuterocoel *sui generis.*	**Rostrum** with a *head-cavity* which becomes divided in the embryo into right and left portions, the former constituting the *rostral cavity* and the latter the *praeoral pit* of the larva and the *ciliary complex* at the roof and sides of the oral hood in the adult. The *praeoral pit* represents, *inter alia*, the *coelomic orifice* of I., being removed from dorsal surface by intervention of notochord; physiologically it is comparable with the dorsal tubercle of II.
Proboscis pore-canal which, as indicated above, opens externally near to or in common with the anterior *neuropore.*	**Neuro-hypophysial canal** or duct of the subneural gland. It arises in primary continuity with the wall of the cerebral vesicle with which it remains in communication in the larva by an *intracerebral orifice*; at the other (oral) end it opens into the vestibule of the branchial sac by an *intrabuccal orifice* which gives rise to the dorsal tubercle of the adult.	**Olfactory pit** into which the anterior *neuropore* opens in the larva.
Ventral mouth of larva and adult.	**Dorsal mouth** of larva (with which the neuro-hypophysial canal communicates) becoming the buccal siphon of adult.	**Sinistral mouth** of larva (separated together with the *praeoral pit* from association with the neuropore by intervention of notochord) becoming the median ventral *velum* in the adult, the innervation of which, according to the discovery of Professor Van Wijhe, remains sinistral.

Having obtained the necessary permission from the authorities of the French administration I left Nouméa on July 18 on board a local steamer for the Isle of Pines, accomplishing the journey of 65 miles in nine hours. The southern coast of New Caledonia is studded locally with forests of *Araucaria*, and the Isle of Pines is a hilly satellite of the larger island, and likewise affords some exquisite coast scenery. It is used as a penitentiary establishment, the native population being confined to a reservation on one side of the island, the most picturesque side, where it is controlled by the Mission authorities under the direction of Père Lambert, who is a renowned conchologist. I paid several visits to the native who was the nominal chief of the tribe, but he failed to understand my wishes and showed me no hospitality. I made an abortive attempt to reach his heart by means of a present, which he accepted, and sent a man in brass buttons to me on the following day to know what it was for.

Altogether I found the Isle of Pines an unsatisfactory place in which to pursue my special and peculiar avocation, and the eighteen days which I spent here were only relieved by two circumstances, namely, the opportunity of studying *Ptychodera flava* which I found at low tide in sandy rock pools on the coralline platform at the base of the cliffs where the breakers expend their fury, and secondly the companionship of my native servant, an important chief from Lifu who had been exiled from his native place for drunkenness accompanied by violence. A man of forty with a distinguished face and bearing, speaking fair English and better French, he served me well in return for his food and one franc a day. He would have made an ideal "roi de Lifu" but for his addiction to the vile vitriol which does duty for liquor. He answered, temporarily, to the name of Eugène, and in the course of conversation he strongly urged me to make for Lifu rather than Maré, although I had been thinking of the latter. Fortunately his counsels prevailed and I left the Isle of Pines on August 5 in a cutter manned by Maré islanders. We anchored for the night at a point called Gadji, at the northern end of the Isle of Pines. Here there are extensive reefs, mud-flats, quicksands and sand which is strongly elastic, rebounding to the tread like india-rubber, imparting an unusual and somewhat exhilarating sensation. There are also numerous islets clothed with vegetation and undermined in a characteristic manner by the action of the sea[1].

The next morning at 4 a.m. we left Gadji with the rising of the moon and had a fair wind to Maré, where we arrived at sundown. There is some difficulty in landing here as the rock-bound coast drops sheer into the sea, and the rudeness of the rocks simply anticipates the astonishing inhospitality of the natives. It is true I presented a dilapidated appearance, especially after walking over the scraggy limestone surface of the island, and had it not been for the good offices of a petty chief called Wainani, who had been a fellow passenger on the cutter, I should have been in a still more desolate condition, being already mistaken for a *libéré*. The Government representative on Maré was the Commandeur, M. Journot, who entertained me at luncheon on my way to the great chief Neisselin at Nētchi. With the best will my friend Wainani none the less led me into a trap, by which I became exposed to the merciless and humiliating diatribes of Neisselin's wife, delivered in excellent English. The population of Maré consists of Catholics and Protestants, and the latter have for some years been left without a white shepherd, but they conduct their own services with a gusto which must be heard to be appreciated.

Besides the usual beehive huts they have white plaster houses which are rather oppressive. I boarded with a native called Ito Pupu and after prayers went to bed. Next day he informed me that his father had partaken of white man. I had agreed with a tall handsome bearded native called Waiyowara, the owner of a cutter, for my passage to Lifu, the arrangement being that he would call for me at a certain place and time. He was not punctual, and such was my anxiety to leave this island where

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[1] Similar mushroom-shaped islets occur in the Fijis and have been described and figured by Mr J. Stanley Gardiner in the *Proc. Camb. Phil. Soc.*, Vol. IX. Part 8, 1898; see p. 459.

I had suffered so much mortification, that I shipped in a small half-decked cutter called the "Marie Therese," with a dangerous native called Pedro as skipper. The boat manifested a pronounced tendency to capsize, and had actually turned turtle on a previous occasion when several Isle of Pines men were drowned. We did not clear the point of Maré without a mishap, as the boat, failing to respond when we were coming about, was driven upon a reef-patch, where she toppled over on her beam-ends. By poling and shoving we managed to escape on the crest of a wave and put back in a leaky condition to Nētchi.

My only course now was to reopen negotiations with Waiyowara, and by dint of allowing him a just measure of reproach and other concessions he consented to land me at Chepenehe on Lifu, where I had been informed a trader, Mr James Wright, had a station. After reporting myself, upon arrival, to the French Resident, I arranged to stay in a small outhouse belonging to Mr Wright and take pot-luck with him for my food. I stayed here for some eight months, in the course of which some *Nautili* which I had succeeded in keeping alive in captivity deposited their eggs in my cages. Most unfortunately these eggs proved to be infertile, an eventuality which the marine zoologist rarely expects to encounter, though it would not surprise an ornithologist.

The wanderings which I have described in the foregoing pages were all directed to one end. I wished to find a locality where *Nautilus* could be both captured and kept prisoner in a moderate depth of water, in four or five fathoms instead of forty or fifty. Here on the shore of Sandal Bay, Lifu, I had come upon the ideal ground for which I had been searching.

The rocky shore at this part of the bay is riddled with a labyrinth of creeks, crannies and blowholes. In calm weather some of these natural tanks present a tempting appearance as if constructed for the benefit of a vagrant naturalist. I soon found however that the wash of the tide, exerting a powerful suction through the narrow holes and crevices, rendered these pools quite useless for my purposes. Nevertheless the thought occurred to me that it would not be a matter of insuperable difficulty, given proper equipment and organisation, to construct a marine reservoir with concrete walls in which refractory animals might be successfully reared, by being accorded a larger measure of liberty than is possible even in the best fish-trap. Such a tank could also be made to serve useful purposes, as for example the breeding of Holothurians from which trepang or bêche-de-mer is prepared. Unless the eggs of *Nautilus* are destined to be taken in a fertile condition at Negros in the Philippines I can offer no other suggestion than the above for the benefit of future naturalist-venturers.

Almost any kind of animal bait may be used to attract *Nautilus* to the fish-traps. Accompanied by my man Saono, an excellent woodman, boatman and diver, I made frequent excursions into the bush to procure land-crabs, which live in holes in the ground beneath stones and logs. To the experienced eye their presence can be known without turning over a stone, by the neatly cleaned and levelled threshold made by the crabs at the entrance to their retreats. When the stone is removed the crab may be at the top, in which case it scampers away, or it may be in the hole, which is perhaps a foot long but only a few inches below the surface. The females of these crabs pass into the "berried" stage in November and December when they troop down to the sea to deposit their larvae in the water. Their migration takes place about the time of the fructification of the ferns, when also the yams which have been planted for the ensuing season begin to shoot up. At this time they, as well as *Birgus*, are taken on the shore by torchlight in hundreds, and are cooked and eaten.

Another bait which may be used when others fail consists of crushed sea-urchins, especially the *Heterocentrotus* (*Acrocladia*) *mammillatus*, which abounds on the reef-patches and is also eaten by the natives. The best bait is made by cooking the large prawns or langoustes, *Palinurus* (also *Scyllarus*), which especially frequent the weather side of the island. When ready they are pounded to a pulp and then wrapped up in the dead fibrous spathes of the cocoa-nut tree, and placed in the basket, to which they impart an irresistible bouquet.

Having observed that the newly captured *Nautili* adhered with great force by means of their tentacles to the sides of the vessels in which they were placed, I fixed some boxes in the cages. They attached themselves to the boxes but made no other use of them, and one day a huge conger eel effected an entrance into the trap and brought serious dissension into the household. To avoid a recurrence of such a disaster we closed up the entrance with sacking. On the next morning there was a curious white object, looking at first sight like some part of the axial skeleton of a bony fish, adhering to the sacking. Upon removing it we found that it had been tightly fixed to the sacking, and very soon I realised that it was the first egg of *Nautilus* which rewarded my gaze. After two years of anxious groping in the dark it may be imagined what a thrill passed through my marrow, destined to be quenched when I found during the course of the following weeks that all the eggs which I attempted to rear were infertile.

I kept my culture cages at a depth of about three fathoms and fed the company of *Nautili* three times a week, going out on Saono's raft for the purpose.

The Lifuan rafts are well-constructed and seaworthy (see Fig. 5, p. 699). They are worked by sculling with a long, flattened pole, which passes through a hole in the centre-board at the front of the raft, and are sufficiently wide and buoyant to bear the weight of two men and a large fish-trap between them. Provided that equilibrium is maintained, a rather difficult matter in a choppy sea, the worst accident to be feared is the snapping of the pole. The position of the fish-traps, which are sunk to depths varying from three to eighteen fathoms, is ascertained by dead reckoning, buoys not being employed. They are dimly seen at sixteen to eighteen fathoms on a calm day, and when it is desired to raise them they are skilfully secured by means of a wooden hook, which is lowered from the raft and passed through the meshes. In the "thingit" (the native name for the fish-traps) in which I kept a stock of *Nautilus* I had a door made, through which I was able to get bodily into the cage on board the raft and manipulate at leisure. I had several of these incubators and tried all methods, pairing off the *Nautili* in some, associating them in companies in others, manufacturing dark recesses in sackcloth, all to no purpose. The eggs were all infertile and often simply consisted of the empty capsules without any vitellus inside. Generally, however, the eggs contained a healthy sherry-coloured vitellus, which either suffered no change when left for a fortnight or commenced to addle. It was on December 5, 1896, nearly four months after my arrival in Lifu, that I obtained my first egg and, according to promise, presented Saono with

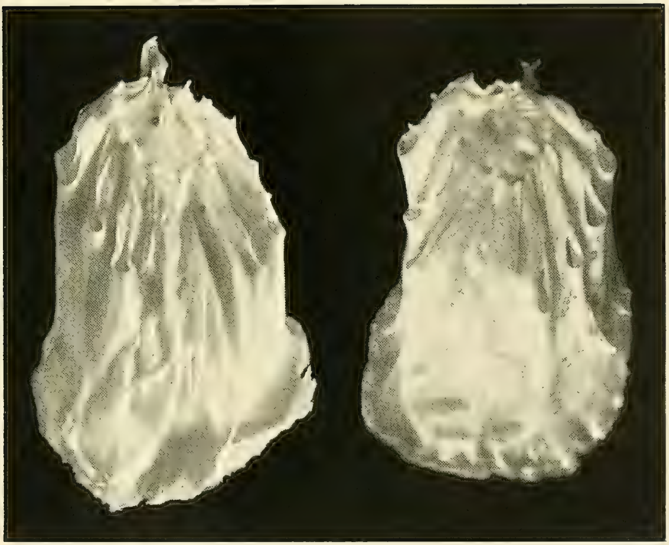

Fig. 18. Two eggs of Nautilus macromphalus from above. × 2.

[*Photographed at the University of Sydney by Mr Grant.*]

To face page 732.

twenty-five francs. Near the end of January, 1897, we had a visitation of wind, probably the trail of a hurricane, which played havoc with my baskets, and cost the lives of some sixteen *Nautili*. Shortly afterwards I lost another "thingit" containing six pairs of *Nautili* in forty fathoms, and on March 8 left Lifu in a small schooner, bound for Nouméa, calling at Uvea on the way.

Apart from *Nautilus* I obtained many valuable accessions to my general collection at Lifu. A large proportion of Sandal Bay is flanked by terraced limestone cliffs from seventy to a hundred feet in height. The base is excavated by the sea, as in the case of the mushroom-shaped islets which I have previously mentioned, and halfway up the face of the cliff there is an exactly similar excavation. From the base of the cliff the water deepens rather rapidly to about forty fathoms, and then there is a sudden drop, showing the existence of a remarkable submarine ledge of dead, shaly rock. I dragged along this forty fathom ledge with a grapnel in the hope of recovering one of my "thingits," which had disappeared, and it was here that I found some peculiar calcareous growths which I preserved, although I had no inkling of what their true nature might be, suspecting them rather to be Foraminifera. In Mr J. J. Lister's hands they have proved to represent a very interesting form of calcareous sponge, *Astrosclera*, offering a curious superficial resemblance to the mesozoic Pharetrones[1].

I also described a curious flatworm[2] from Lifu under the name of *Heteroplana*, but the generic properties which I ascribed to it are open to another interpretation. The shape of the body was peculiar, symmetrical in front, not quite symmetrical behind, unlike anything else I had seen.

Examination with lens and microscope in the living state revealed the fact that the organs of the left side, principally the intestinal diverticula, were suppressed. I found the worm in a hole on the lower side of a coral block[3] and on account of its large size, semi-opaque orange colour, characteristic shape and other peculiarities, gave it the above name. It has been suggested that *Heteroplana* is a phase in the regeneration of a mutilated Polyclade worm. If this be so I cannot account for its very definite external form, but at any rate the genus must remain in abeyance until more light is thrown upon this subject[4].

The population of Lifu, like that of the other Loyalty Islands, is now entirely Christian, being divided between the Catholic and Protestant communions. The two great hereditary chiefs of the island, Ukenesoe and Bula, who formerly waged incessant warfare with each other, are now the respective champions of the rival creeds. The social organisation is somewhat communistic so far as this is compatible with the existence of chiefs, and it sometimes happens that even such valuable property as a horse is readily yielded up to the first importunate acquaintance who casts envious eyes upon it. But of course a return present will be exacted sooner or later. If I gave something of value, tackle, food or money, to my man, it was quite a chance if I did not find it shortly in the possession of somebody else in whom I had no particular interest.

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[1] See Appendix.

[2] I collected a number of Polyclade worms which I have sent to Prof. A. Lang at Zurich. For notes on oviposition of Polyclades cf. Willey, A., "Letters from New Guinea," *Quart. J. Micr. Sc.*, Vol. xxxix.

[3] Repeated and laborious search failed to elicit any more specimens.

[4] Cf. C. Rina Monti, "La rigenerazione nelle Planarie marine." *Mem. Ist. Lombardo*, xix. 1900.

Unless some epidemic should come to decimate the population, the future welfare of the Lifu natives seems to be insured by the poverty of the land. No primary rocks occur at any part of the island, which consists entirely of coralline limestone with patches of arable soil, capable of producing a certain amount of food to support a population of about 7,000, which number appears to remain fairly constant.

I finally left Nouméa for Sydney by way of Esafate or Sandwich Island in the New Hebrides on March 28th, 1897. A few days after my arrival for the second time in Sydney, I despatched the following cable to Professor Alfred Newton, F.R.S., Chairman of the Balfour Managers:—"No stages, shall I spend rest of year New Britain?" to which I received an affirmative reply. Accordingly I set about making preparations for a fresh campaign in New Britain, the principal addition to my apparatus being a nest of seven large hencoops, which were made according to my instructions at the Blind Asylum in Sydney.

I now pass on to the concluding episode of my voyage. I landed in New Britain for the second time on June 16th, 1897, and on the following day one of my former crew, To-lara by name, came to see me and agreed to serve with me again. This gave me an important start; I revisited my old haunts in Blanche Bay without delay, and having fitted out my Sydney cages, I stocked them with *Nautilus*-couples as soon as I could procure them. Very shortly I commenced to find the eggs of *Nautilus pompilius* attached to the sacking round the sides of the cages, hardly distinguishable from those of *N. macromphalus* at Lifu. My hopes revived, but I soon found that the eggs fared no better in Blanche Bay at a depth of 30—50 fathoms. No development took place, and in course of time the vitellus commenced to undergo liquefaction and decomposition. I continued my efforts, at the same time accumulating collateral material, until the following September, when I bade adieu to New Britain, and thus terminated my long quest.

APPENDIX.

Mr J. J. Lister, F.R.S., has favoured me with the following additional note, "On the mineralogical character of the skeleton of *Astrosclera*," which he has received from Mr Hutchinson of Pembroke College, Cambridge.

"A short time after the publication of the description of the mineralogical characters of the skeleton of *Astrosclera willeyana*, an important paper was communicated to the Mineralogical Society by Miss Agnes Kelly, entitled "Conchite, a new form of Calcium Carbonate" (*Min. Mag.*, Vol. XII. p. 363, 1900). In this paper the authoress claims to have established the existence of a form of calcium carbonate distinct from calcite and from aragonite, and to have shown that all calcium carbonate of organic origin, formerly believed to be aragonite, really belongs to the new variety.

"The specific gravity of conchite is given as 2·830—2·865. It is uniaxial and negative. Its birefringence is less than that of calcite, and the maximum value obtained for its index of refraction $\omega_D = 1{\cdot}661$ is less than either β or γ of aragonite.

"Miss Kelly's conclusions have however been questioned by Brauns (*Centralbl. für Min.*, 1901, 134) and by Vater (*Zeit. für Kryst.*, XXXV. 166), who maintain that conchite is essentially the same as aragonite.

"Meigen (*Centralbl. für Min.*, 1901, 577) has recently shown that aragonite and calcite in fine powder behave differently when boiled with cobalt nitrate solution, the former turning reddish-lilac, while the latter remains white or becomes yellowish. G. Panebianco (*Rivista Min. Ital.*, XXVIII. 5—12) confirms Meigen's observations as regards aragonite but finds that calcite turns sky-blue. *Astrosclera* when submitted to this test gives the colour characteristic of aragonite. The conclusion drawn from the specific gravity determination, that the skeleton of *Astrosclera* is not calcite, is thus satisfactorily confirmed. Its properties as given in my previous description agree with those of conchite, but until the independence of conchite and aragonite is more definitely established, the mineral element present in *Astrosclera* may best be regarded as aragonite.

A. HUTCHINSON."

II. SPECIAL CONTRIBUTION.

With Plates LXXV.—LXXXIII., a Map, and 15 Text-figures.

This is neither the time nor the opportunity for the composition of a costly monograph on *Nautilus*. It will be time when the embryonic stages have been discovered and opportunity when it is possible for an investigator to command the requisite knowledge and material to permit of detailed comparisons being made, step by step, between more or less distantly related types. I am only able to furnish a contribution which partakes of the nature of a monograph in a strictly limited sense of the term. The new matter contained in these pages consists of facts and suggestions some of which have been already published in a preliminary form, and relates principally to the following aspects of the subject:—bionomics (habits, range, oviposition), branchial sense-organs (osphradia), mechanism of respiration, injection of the vascular system, connections of the siphuncle, innervation of the ophthalmic tentacles, development of the accessory sexual organs, enumeration of the digital tentacles, orientation, and specific divergence.

1. Historical Survey.

The bibliography of *Nautilus* includes so many memoirs of the first order of importance written at varying intervals by experienced anatomists of different schools and countries during the last seventy years, as to convey the impression that its conchological, malacological and biological properties must be well-nigh established and that the only scope for further contributions to knowledge must take the direction of physiological and embryological researches. Such however is not the case, and so far as the finer anatomy and œcology of *Nautilus* are concerned it will be long before the Pierian spring is exhausted.

The seven decades which have elapsed since *Nautilus* was assigned its definite position in the natural system fall into two very distinct periods, the first of which was inaugurated by Sir Richard Owen[1] in 1832, followed by Valenciennes[2] in 1841, and terminated by Keferstein[3] in 1865. The second period, which is now in course, was opened by the works of Professors von Jhering[1] (1877—1881), and Lankester and Bourne[2] (1883).

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[1] Owen, R., "Memoir on the Pearly *Nautilus*." Published for the Council of the Royal College of Surgeons, 1832, with 8 plates.

[2] Valenciennes, A., "Nouvelles recherches sur le Nautile flambé (*Nautilus pompilius*, Lam.)." *Arch. Mus. Paris*, II. pp. 257—314, Pl. VIII—XI, 1841.

[3] Keferstein, W., "Beiträge zur Anatomie des *Nautilus pompilius*." *Nachr. Ges. Göttingen*, 1865, pp. 355—375; plates published in Bronn's *Klassen und Ordnungen des Thierreichs*, 1866, in illustration of Malacozoa-Cephalopoda, Taf. CX—CXV.

It is a point of literary interest to note that there is some evidence, which was discussed at length by Owen in his celebrated memoir, tending to show that the mollusc which inhabits the shell of the Pearly Nautilus was known to the father of natural history. However this may be, it is certain that since the revival of learning, *Nautilus* has on two occasions, separated from one another by an interval of a hundred and twenty years, been the subject of an important zoological discovery. The first of these was made by a Dutch physician and botanist, resident in the East Indies, named George Everard Rumph, usually known as Rumphius, the author of a large work entitled *D'Amboinsche Rariteitkamer*, which was published in folio in Amsterdam in 1705, and was translated into German sixty years later. In this volume appeared the first recognisable description and illustration of *Nautilus pompilius*, this fact constituting, I believe, one of his principal titles to enduring distinction as a zoologist.

Rumphius described some of the external characters of *Nautilus* with considerable accuracy, recognising it as a Cephalopod Mollusc allied to the calamaries, cuttle-fishes and octopuses, but his statements lacked confirmation and amplification and consequently had no marked effect on classification. Cuvier [*Règne Animal*, III. p. 366, quoted by Owen] dismissed his figure of *Nautilus* with the epithet "indechiffrable," but Keferstein [*Nachr. Ges. Göttingen*, 1865, p. 356] was more generous, saying, "Oken allein scheint mir diese recht gute Beschreibung und Abbildung angemessen gedeutet zu haben."

The works of Rumphius[3], overshadowed by those of Linnaeus, became practically forgotten, and so it happened that the capture of a unique specimen in the year 1829 by Dr George Bennett off the island of Erromanga in the New Hebrides, followed by its successful transmission to Europe, had all the merit of an original discovery[4]. In his book entitled *Gatherings of a Naturalist in Australasia*, Bennett tells us that his attention had been directed to the subject of *Nautilus* and its relation to Ammonites and Belemnites after a chance conversation with Professor Owen.

In the evening of August 24th, 1829, while at anchor in Dillon Bay, Erromanga, he "observed an object floating upon the water, resembling a dead tortoiseshell cat. So unexpected a sight," he says, "excited my curiosity, and the boat...was immediately... sent to ascertain the nature of this floating object. It was found to be the Pearly Nautilus.... On being brought on board, I observed it retract the tentacles or feelers still closer than before; and this, with a slight quivering of the body, was the only sign of vitality it gave." This specimen was therefore clearly in a moribund condition at the time of its capture. Professor Owen, we are told, received the prize and went to Paris to see Cuvier. But Cuvier died shortly afterwards in the same year which witnessed the publication of Owen's memoir, without having had the opportunity of satisfying his instinct of naturalist by the sight of this remarkable creature.

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[1] Jhering, H. von, *Vergleichende Anatomie des Nervensystems und Phylogenie der Mollusken*, Leipzig, 1877; "Ueber die Verwandtschaftsbeziehungen der Cephalopoden." *Zeitschr. wiss. Zool.*, Bd. XXXV. pp. 1—22, 1881.

[2] Lankester, E. R., and Bourne, A. G., "On the existence of Spengel's olfactory organ and of paired genital ducts in the Pearly *Nautilus*." *Quart. J. Micr. Sc.* XXIII. pp. 340—348, 4 figg. 1883. Other figures were published in the same year in Professor Lankester's article "Mollusca," *Encycl. Brit.*, 9th ed., and reissued in his *Zoological Articles contributed to the Encyclopaedia Britannica*, 1891.

[3] In addition to the *Rariteitkamer*, he wrote the *Herbarium Amboinense* which was edited and published after his death by J. Burmann, Amsterdam, 1741—1755.

[4] Bennett, G., "The inhabitant of the Pearly Nautilus." *London Medical Gazette*, VIII. p. 729, 1831; also by the same author, *Gatherings of a Naturalist in Australasia*; London, 1860, pp. 374 *et seq.*

2. External Form and Pigmentation.

The external appearance of *Nautilus* is too familiar to require formal description, especially since an excellent set of drawings representing living specimens in different attitudes has recently been published by Professor Bashford Dean[1].

The complete animal consists of the shell and its tenant or, in New Britain parlance, the "pal-a-līalīa" and its "wirūa," the two being inseparable until parted by death. Although the body is firmly bound to the shell by the tension of the paired columellar muscles, it is not really attached to the shell, the ends of the muscles being covered over with a horny membrane continuous with a horny girdle, so that when the pressure of the muscles is overcome, the entire animal, including the siphuncle, may be removed without lesion, except that the membrane is generally lacerated. The fact that the muscles are not directly attached to the shell was pointed out by Owen

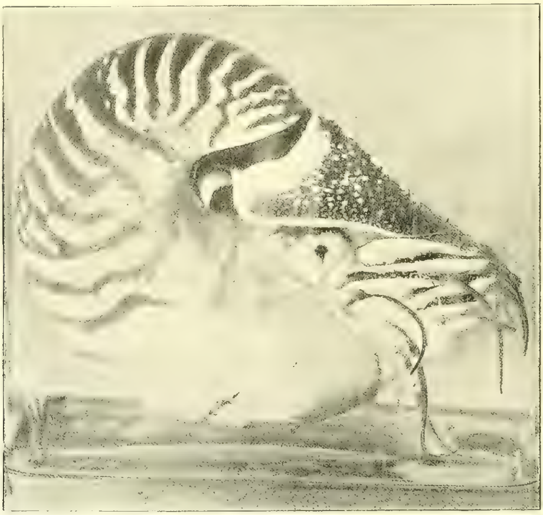

Fig. 1. *Nautilus pompilius*, L., photographed from life in New Britain, 1895. [Reproduced from the *Quart. J. Micr. Sc.*, Vol. xxxix. 1896, p. 179, by permission of the Editor.] About one-half natural size.

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[1] Dean, B., "Notes on Living *Nautilus*." *Amer. Natural.*, xxxv. pp. 819—837, 1901. The material was collected in the strait between the islands of Negros and Cebu in the Philippines.

and by Vrolik[1], but the latter erroneously supposed that the animal was attached to the shell by means of the siphuncle, presumably because the latter became broken off during the removal of his specimen from the shell.

Whether at rest or on the alert, the dark brown and whitish mottled or piebald coloration of the exposed part of the molluscous body harmonises well with the zebra-like markings on the shell. This scheme of pigmentation apparently produces the same effect as does the play of light on the surface ripples of the sea, and the alternating light and dark bands of the shell might be appropriately described as ripple-markings.

On one occasion when on a raft with my native servant in Sandal Bay, Lifu, I accidentally dropped a sprightly *Nautilus* overboard in four or five fathoms of clear water. It instantly disappeared in a miraculous manner, baffling all our efforts at recovery. Whether the gleam of colour would confer an equal degree of invisibility in the phosphorescent twilight at greater depths it is of course impossible to say, but when the active migratory habits of *Nautilus* are considered and also the fact that it is subject to the attacks of voracious fishes, probably sharks and congers, as is evidenced by the mutilated condition of many individuals, I think the above observation may be taken to indicate that the colour-markings, being what they are, exert a protective influence.

Under certain conditions, more frequently when kept in a confined space, I noticed that a great portion of the brown pigment would disappear from the outer surface of the hood, so that the latter became partly, in some cases entirely, bleached. The pigment would seem to be actually discharged from the epidermal cells in which it is normally lodged in an even layer near their outer ends.

The wart-like, generally whitish, gibbosities on the upper surface of the hood, have been regarded as sensory papillae, and were likened by Van der Hoeven (1848) to the *papillae vallatae* of the human tongue. It is obvious, however, that they are not sense-organs.

In the retracted state the mouth of the shell is closed by the thick warty hood, which forms the upper part of the cephalic complex and acts as an operculum. In this condition the hood somewhat resembles the foot of a Gastropod, and Rumphius stated that when the animal crawls the hood is directed downwards, and the side which is uppermost in the attitude of swimming becomes a plantar surface when creeping.

This mistake was repeated by Owen, who described the hood as being of a fibrous texture and white colour internally, resembling dense *corium*, but added that it is "doubtless muscular, and in creeping (the position of the animal being reversed) seems calculated to act as its chief locomotor organ." It is true that the hood is traversed by thin and sparse muscular fasciculi, but its structure is essentially coriaceous, and it serves as a shield, not as an organ of locomotion.

In the attitude of swimming and breathing, as shown in the photograph here reproduced, the hood is raised above the margin of the shell so as to expose the tentacles, the funnel and the eyes, and to allow of free communication between the mantle-cavity and the external aqueous medium. In the figure the front end of the funnel may be faintly detected projecting beyond the anterior lip of the shell. The posterior surface of the hood is concave, in accurate correspondence with the involute convexity (*anfractus*) of the keel of the shell, and in the concavity there is a semilunar fold which fits upon the blackened involute portion of the shell, towards which it acts as a lubricant. This fold is the *nuchal membrane* which was compared by Keferstein (1865), and Lankester (1883, *Encyc. Brit.*) with the cartilaginous nuchal plate of *Sepia*. I shall have occasion to return to it later. In the specimen which I photographed, the slender tentacles were mostly in a condition of protraction, and when, as in this instance, the animal is stationary although expanded, they are seen to hang down listlessly, but when swimming vigorously backwards are held out straight[1], like the arms of *Octopus* under the same circumstances.

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[1] Vrolik, W., "On the Anatomy of the Pearly Nautilus." *Ann. Nat. Hist.* XII. 1843, pp. 173—175.

3. Sexual Dimorphism.

1848. Van der Hoeven, J. Eenige afwijkingen in den vorm van het hoofd, waargenomen bij een mannelijk voorwerp van *Nautilus pompilius*. Tijdschr. voor de wis- en natuurkundige Wetenschappen, Deel I. p. 67, Pl. 1, figg. 1—3. Amsterdam.

1850. Van der Hoeven, J. Contributions to the knowledge of the animal of *Nautilus pompilius*. Tr. Zool. Soc. London, Vol. IV. part I. pp. 21—29, Pl. V—VIII.

1856. Van der Hoeven, J. Bijdragen tot de ontleedkundige kennis aangaande *Nautilus pompilius* L., vooral met betrekking tot het mannelijke dier. Verhandel. der kon. Akad. Amsterdam, Deel III., 20 pp., 5 plates.

1883. Bourne, A. G. The differences between the males and females of the Pearly Nautilus. Nature, XXVIII. p. 580.

1895. Willey, A. In the home of the *Nautilus*. Natural Science, Vol. VI., June, 1895, pp. 405—414.

1895. Vayssière, A. Sur le dimorphisme sexuel des Nautiles. C. R. Ac. Paris, June, 1895, Tome 120, pp. 1431—1434.

1901. Dean, B. Notes on living *Nautilus*. Amer. Natural. XXXV. pp. 819—837.

In *Nautilus* the sexes are separate, as in all other Cephalopoda, and this dioecism is accompanied by a sexual dimorphism which is determined by the nature of the accessory organs of reproduction and is manifested in the dimensions of the mouth of the shell.

With regard to the statistical relations of the sexes I found that, judging from the specimens taken in the traps, the number of males exceeds that of the females in the case of *N. pompilius*, while for *N. macromphalus* the reverse was true. The excess of females, or hyperpolygyny, is a common phenomenon among Cephalopoda, and it is a curious fact that there should be an apparent difference in this respect between these two species of *Nautilus*. The figures relating to the former species which I have recorded are perhaps more convincing than those which concern the latter. Out of 216 specimens of *N. pompilius*, 150 were male and 66 female. Of 26 *N. macromphalus*,

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[1] This is well shown in some of Dr Dean's figures to which I have already referred.

10 were male and 16 female. The actual distribution of the numbers for *N. pompilius* is given in the subjoined table.

Date		Total	Male	Female	Locality
1895.					
January	18	14	12	2	Blanche Bay
„	22	21	16	5	„
„	24	8	3	5	„
February	7	22	15	7	„
March	2	2	1	1	„
„	6	6	4	2	„
„	7	29	22	7	„
„	15	10	9	1	„
„	16	6	5	1	„
„	19	17	8	9	„
„	30	4	3	1	„
April	20	10	8	2	„
„	25	7	4	3	„
May	21	7	5	2	„
„	24	1	1	0	„
„	28	1	1	0	„
June	13	4	2	2	„
„	26	6	3	3	„
August	20	5	5	0	Talili Bay
September	13	5	5	0	„
„	14	6	4	2	„
1897.					
July	7	5	2	3	Blanche Bay
„	8	14	8	6	„
„	9	6	4	2	„
		216	150	66	

In contrast with the race of the Argonauts or Paper Nautili where the male is strikingly smaller than the female, which alone carries a shell of peculiar construction, the males of the Pearly *Nautilus* are rather larger than the females. This predominance of the male is due to its possession of a remarkable organ, the *spadix*, placed beside the mouth within the outer whorl of tentacles and formed, as first described by the Dutch anatomist Van der Hoeven, by the combination of four modified tentacles belonging to the inner whorl (see below). The presence of the bulky spadix in the midst of the cephalic complex which, in the retracted condition, is concealed below the hood, determines an increase in the dimensions of the latter, which must obviously find expression in the size of the orifice of the shell.

The sexual dimorphism is more pronounced in *Nautilus* than in any other recent Cephalopod, with the exception of *Argonauta*, owing to the fact that the *spadix* is a permanent structure, having a gradual development from the adolescent to the adult stages. It is not periodic in its appearance as is the *hectocotylus* of the Dibranchs. That its presence should determine a difference in the shape and dimensions of the orifice of the shell, is a fact which has already been made use of by palaeontologists, who now recognise similar sexual variations in the shells of extinct species. Commenting upon my observations and figures (published in 1895) relating to the shells of male and female *Nautilus*, Professor Howes[1] pointed out that these and the nearly contemporaneous observations of M. Vayssière bore out the suggestion made by D'Orbigny more than fifty years ago that certain differences in the shells of Ammonites might possibly be indicative of sexual variation.

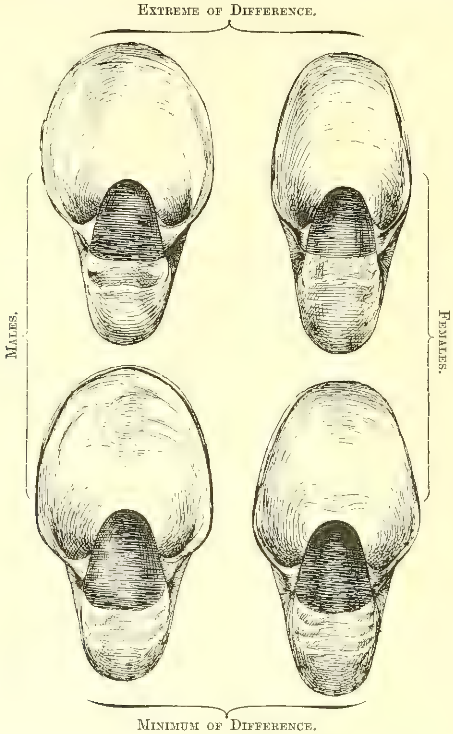

FIG. 2. Secondary sexual characters in shells of *Nautilus pompilius*.
[Reproduced by favour of Dr F. A. Bather from *Natural Science*, Vol. VI. 1895, p. 411.]

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[1] Howes, G. B. Address of the President, *P. Malac. Soc. London*, Vol. II., 1896—1897, see pp. 69—71.

The sexual dimorphism manifested by the shells of recent *Nautilus* has also been observed among the much more numerous species which occur in the fossil state. For example, it is shown in a striking manner in the figures of *Nautilus bradfordensis* Crick, contained in an article by Mr G. C. Crick[1], where he described and figured the shells of eleven species of *Nautilus* taken from various zones in the Inferior Oolite of Dorsetshire, of which no fewer than ten were registered as new to science.

4. Species and Range.

1855. Sowerby, G. B. Monograph of the genus *Nautilus*. Thesaurus Conchyliorum, Vol. II. pp. 463—465. Pl. XCVII. and XCVIII.

1855. Macdonald, J. D. On the anatomy of *Nautilus umbilicatus* compared with that of *Nautilus pompilius*. Phil. Trans. 1855, pp. 277—288, 2 plates.

1857. Gould, A. A. On the true *Nautilus umbilicatus* of Lister. P. Zool. Soc. London, XXV. 1857, pp. 20, 21.

1859. Bennett, G. Notes on the range of some species of *Nautilus*, on the mode of capture, and on the use made of them as an article of food. P. Zool. Soc. London, XXVII. 1859, pp. 226—229.

[In this paper Bennett erroneously speaks of *N. macromphalus* as occurring in the New Hebrides.]

1860. Bennett, G. Gatherings of a Naturalist in Australasia. (London, J. Van Voorst, p. 374.)

1877. Bennett, G. Notes on the Pearly *Nautilus* [*N. pompilius*], Ann. Nat. Hist. (4), Vol. XX. pp. 331—334.

1896. Vayssière, A. Étude sur l'organisation du Nautile (caractères zoologiques, dimorphisme sexuel, tentacules et spadice). Ann. Sci. Nat. (8), II. pp. 137—186. Pl. 16—19.

[Includes critical examination of the radulae of *N. pompilius* and *N. macromphalus*; Vayssière quotes D'Orbigny (1846, Dictionnaire universel d'hist. nat., Article "Nautile") to the effect that *N. pompilius* occurs at the Nicobar Islands "dont les habitants fument et boucanent sa chair."]

1896. Willey, A. Zoological observations in the South Pacific. III. On some variations in the shell of *Nautilus*, with description of a new variety. Quart. J. Micr. Sc., XXXIX. pp. 227—230, with figures on Pl. 13.

1898. Willey, A. Some zoological results of a voyage to Melanesia during the years 1894—1897. [*N. umbilicatus.*] P. Cambridge Philos. Soc., IX. p. 398.

Hitherto it has only been found really practicable to differentiate the recent species of *Nautilus* according to the character of the shell in the umbilical region, and from this point of view four well-marked forms have been distinguished, namely, *N. pompilius* Linn., with umbilicus concealed by a deposit of callus in the adult, *N. stenomphalus*

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[1] G. C. Crick, 1898, "Descriptions of new or imperfectly known species of *Nautilus* from the Inferior Oolite, preserved in the British Museum (Natural History)." *P. Malac. Soc. London*, Vol. III. pp. 117—139, 1898. Cf. also Buckman, S. S., and Bather, F. A., "Can the sexes in Ammonites be distinguished?" *Nat. Sci.*, Vol. IV., June 1894, p. 427.

Sowerby, with narrow perforate umbilicus, *N. macromphalus* Sowerby, with rather wide subperforate[1] umbilicus, *N. umbilicatus* Lister, with very wide perforate umbilicus.

Judging from the known facts relative to the coiling of the shells of extinct Ammonoids and Nautiloids and also from the fact that the young shells of *N. pompilius* are perforate, the umbilical region becoming subsequently covered over by callus, I suppose it is natural to conclude that the form of the shell in *N. umbilicatus* is the most primitive among recent species, while that of *N. pompilius* is the most highly adapted.

If inquiry be made into the nature of the adaptation which has resulted in the complete closure of the umbilicus in the latter species, it will be found as a fact that an exposed deeply excavated umbilical region, such as is presented by the shells of *N. macromphalus* and *N. umbilicatus*, is liable to be selected as a nidus for the attachment of all kinds of sedentary animals, Serpulids, Cirripedes, Ostreids, Bryozoa, Foraminifera, and others.

The fouling of the shell resulting from the incrustations of these foreign bodies will not only serve to irritate the sensitive edge of the mantle in their vicinity, but will also materially hamper the swimming of the *Nautilus*. (Pl. LXXIX. fig. 1.)

The deposition of callus over the umbilicus in *N. pompilius* effectually repels the visits of unbidden guests. In view of these considerations it is interesting to note that it is precisely in the umbilical region that the shell of *N. pompilius* exhibits marked variations, to which I have called attention (1896), and I came to the conclusion that *N. stenomphalus* was simply an extreme variety of this species. Shells which are assigned to *N. stenomphalus* also vary in the diameter of the umbilicus, and I named a form of which I obtained one specimen of the shell only, through the kindness of the Hon. M. H. Moreton, at Samarai, *N. pompilius*, var. *Moretoni*, but I have since been shown a specimen in the Manchester Museum by Mr W. E. Hoyle which is identical with mine.

In 1855 Macdonald described the anatomy of a species from New Caledonia, which he erroneously called *N. umbilicatus*, subsequently recognising his mistake, and correcting the name to that of *N. macromphalus*[2]. Macdonald's investigation of the anatomy of *N. macromphalus* resulted, as is well known, in the discovery of the otocysts, but revealed no appreciable specific differences between it and *N. pompilius* so far as the soft parts are concerned. In fact the animals of these two species are really indistinguishable, and I was therefore very pleased to come into the possession of a single mutilated specimen of *N. umbilicatus* accompanied by its shell, which had been picked up from the surface of the sea, not far from Milne Bay in British New Guinea, and to find that this species differed noticeably from its congeners by the character of the hood, the gibbosities of which have the form of flat-topped angular areas separated by deep grooves, producing a pronounced tessellated appearance. (Pl. LXXVIII. fig. 3.)

In comparison with its former world-wide distribution, evidenced for example by the abundance of its remains in the London Clay, the present restricted range of the genus

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[1] If the shell is coiled in such a manner that a space is left between the first chamber and the first turn of the spiral so that light may be seen through the pin-hole aperture, the umbilicus is said to be perforated. In the shell of *N. macromphalus* there is a pit on each side but it does not extend through from one side to the other.

[2] Macdonald, J. D., "Further observations on the anatomy and physiology of *Nautilus*." *P. R. Soc. London*, VIII., 1857, pp. 380—382.

Nautilus, shown in the map at the end of this article, appears to have a special interest It is wholly confined to the seas adjoining the islands of the Eastern Archipelago, including in the latter term the East Indies, Philippines, New Guinea and its dependencies, Solomon Islands, New Caledonia, New Hebrides, and Fiji. Its shells have been picked up on the Nicobar Islands, Japan [Dean] and the coast of New South Wales, drifting to these localities which lie outside the range of the living animal.

It is curious that so far as is known with any certainty it does not occur west of the Strait of Malacca nor east of Fiji. Although it descends to deep water, the single specimen obtained during the Challenger Expedition having been dredged in 320 fathoms[1], it is not an abyssal form, but rather seems to affect the vicinity of large islands, which perhaps in former ages were united to still larger continental masses. Mr Charles Hedley, who has developed a remarkable theory of a Melanesian plateau, which amongst other connections united New Caledonia to New Zealand (as indicated primarily by the distribution of land-molluscs), in a recent paper says, "It is remarkable how strictly *Nautilus* observes as its eastern limit the ancient coast line of the Melanesian plateau[2]."

If the generic distribution is interesting, the local range of one of the three recent species, namely *N. macromphalus,* is still more strange. Although as noted above there is no apparent difference between the animals which construct the shells of *N. pompilius* and *N. macromphalus* respectively, yet these species are quite distinct, as is shown not only by the coiling of the shell, which is quite constant in the latter, but also by their geographical distribution. *N. pompilius* is never taken in the New Caledonian Group [New Caledonia, Isle of Pines, Loyalty Islands], and *N. macromphalus* is never taken anywhere else. The species which occurs among the New Hebrides and Fiji Islands is *N. pompilius.* When we consider the individual abundance of *Nautilus* wherever a favourable locality is known, the circumscribed limits of the area frequented by *N. macromphalus* alone are very puzzling. On the other hand so far as we can judge from the scanty data which are available, the area of distribution of *N. umbilicatus* overlaps that of *N. pompilius,* and therefore this factor does not contribute to the differentiation of the species, but in this case the animals are quite distinct, *N. umbilicatus,* as I have already mentioned, presenting a characteristic areolation of the upper surface of the hood, resembling the pallial investment of *Lepidoteuthis grimaldii* described by M. Joubin[3]. The same description applies to both sets of cutaneous structures, rhombohedral scales of cartilaginous consistency and fibrous texture. Of course they have been independently acquired, since they occur in different regions of the body, on the cephalopodium in *N. umbilicatus,* on the mantle in *Lepidoteuthis.*

It follows from what has preceded that the recent species which has the widest known range is *N. pompilius,* since it occurs in the Philippines, Moluccas, Bismarck Archipelago, Torres Strait, New Hebrides, and Fiji. The other species which can be obtained in abundance is confined to the New Caledonian Archipelago, namely, *N. macromphalus.* Finally, the third species *N. umbilicatus* occurs also in Papuan waters, but the animal has only been taken once. Its shell is occasionally drifted upon the shores of New Britain and elsewhere, but it is much rarer than the others, and is often spoken of as the "king *Nautilus*[1]."

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[1] Moseley, H. N., *Notes by a Naturalist on H.M.S. Challenger.* Edition of 1892, p. 256. (First edit. 1879.)

[2] Hedley, C., "Descriptions of new Mollusca, chiefly from New Caledonia." *P. Linn. Soc. N. S. Wales,* 1898, Part I., see p. 100.

[3] *Campagnes Scient. Prince de Monaco,* 1900, Cephalopoda, p. 70, Pl. xv. fig. 2.

5. Mantle; Shell; Nuchal membrane.

Under the above heading I shall speak of the formation of the septa which results in the incameration of the shell. The relative importance of this subject may be estimated from the fact that there is an apparently widespread belief which requires correction. It has been suggested, and I think in some quarters adopted as a dogma, that the formation of successive septa is correlated with the recurrence of reproductive periods. This is not the case since, according to my observations, propagation only takes place after the last septum has been formed. Furthermore in spite of the numerous publications which have dealt with the mantle, and the still more numerous treatises on the shell of *Nautilus,* there is not one paper that I have been able to consult in which the delimitation of the mantle in its relation to various parts of the shell is quite clearly displayed. The relations of the mantle to the animal are now well known and have been so for many years, although in one respect they were erroneously described by Owen (1832), who has the following statement, which must appear strange to all who have handled the animal. He says on p. 9 of his memoir:—"At the ventral aspect of the body the mantle becomes thinner, is prolonged anteriorly, and *is perforated by a large aperture through which the funnel passes*" [italics mine]. This is one of three principal mistakes[2] contained in Owen's otherwise wonderful monograph, which was based upon the dissection of a single specimen, and it is perhaps permissible to refer to them, not for the purpose of animadversion but rather for instruction and encouragement.

The mantle is transparent in the living animal (cf. Pl. LXXV.) and consists of two portions, an anterior free pallial fold, which encircles the fore-part of the body like a collar; and a posterior portion, which forms the thin membranous integument of the visceral sac, to which is added an appendix called the siphuncle[3].

The integument of the visceral sac has always been reckoned as part of the mantle on account of the fact that the whole of the mantle area is capable of secreting nacreous substance externally, the posterior or visceral portion in particular being concerned with the formation of the septa. The growth of the shell takes place at the free border of the pallial fold, but the whole outer surface of the fold can deposit nacre, as is indicated by the occasional appearance of nacreous intumescences on the inner surface of the shell, and also by the rare occurrence of the phenomenon of true pearl-formation, one example of which came under my observation.

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[1] No impression of the contrast between the former and the present distribution of *Nautilus* as a genus can be better obtained than by an inspection of the superb collection of Jurassic, Cretaceous and Tertiary *Nautili* which is exhibited at the British Museum (Natural History). Compare also the following publications:—*Catalogue of Fossil Cephalopoda in the British Museum,* Part I. (1888), by A. H. Foord; Part II. (1891) by A. H. Foord; Part III. (1897), by A. H. Foord and G. C. Crick. Some seventy species of *Nautilus* are enumerated in the *List of the types and figured specimens of Fossil Cephalopoda in the British Museum* (Natural History) by G. C. Crick, 1898.

[2] The other two are the description of non-existent peripheral ganglia and the assertion of a communication between the siphuncle and the pericardium and thence to the exterior through the viscero-pericardial apertures.

[3] See below.

Upon taking a shell, of which the animal had died and fallen out, from a basket at Lifu, something rattled like a stone in the shell. It turned out to be a handsome pearl of large size, but of doubtful value as a gem, since the shape is not quite regular, flattened on one side, and the surface is not absolutely pure. It measures about 15 millimetres in major diameter, 11 mm. in height, weighs 3690 milligrammes and is, I believe, the first nautiline pearl to be recorded.

The shape of the shell, a circinate spiral, belongs to one of those fundamental forms which recur both primarily and secondarily under various guises in both kingdoms of the organised creation. This form is calculated, for example, to meet the requirements of economy of space combined with strength and symmetry of construction, and has therefore a physiological meaning. It is certainly remarkable to find a mollusc provided with an external shell as large as that of *Nautilus*, which is at the same time an expert and rapid swimmer. This faculty of swimming as the principal, practically the sole means of locomotion, depends of course more upon the buoyancy of the shell than upon its shape, but the latter should not be disregarded in this connection.

The buoyancy of the shell is due to the series of air-chambers which have long excited the admiration of poets and philosophers. Successive chambers are added by the secretion of fresh septa *pari passu* with the growth of the animal. If the shell, with the live *Nautilus* in it, be perforated over the chambers under water, the air bubbles gently out as the water enters. I regret that I omitted to collect any of this air, but Vrolik (1843) ascertained that it contained more nitrogen than atmospheric air, a fact which is not surprising if we consider that the animal could better afford to part with nitrogen than with oxygen. *Nautilus* seems to have a peculiar faculty of producing gas[1], and my knowledge of the pallial veins was chiefly due to their automatic injection with gas after removal of the animal from the shell.

The chambers are not individually air-tight since they are perforated by the siphuncle, but collectively they are rendered an air-tight and water-tight hydrostatic apparatus, owing to the fact that the animal itself completely closes up the entrance to the chambers in virtue of its adherence to the shell by the muscles and *annulus* (girdle of Owen). Any loss by diffusion might be made good by the siphuncle, but apart from this I see no reason to imagine that the air which fills the chambers undergoes any appreciable fluctuations of pressure. It is, I am convinced, an error to suppose that variations of pressure of the air in the chambers enable *Nautilus* to rise or sink as the case may be. The air simply renders the shell buoyant once for all.

The progressive growth of the animal is accompanied by the addition of new chambers, which give increased buoyancy and so maintain the shell under the entire control of the animal until a limit is reached when the last air-chamber has been divided off, and then only does propagation commence.

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[1] Professor Lankester (Article "Mollusca," *Encyc. Brit.*, Vol. XVI. 9th edit.) says:—"In connexion with the secretion of gas by the animal, besides the parallel cases ranging from the Protozoon *Arcella* to the Physoclistic Fishes, from the Hydroid Siphonophora to the insect-larva *Corethra*, we have the identical phenomenon observed in the closely-allied *Sepia* when recently hatched."

There are several features in the shell which indicate that it has reached its limit of growth and that its inhabitant is therefore mature. The lip of the shell which has hitherto been thin and fragile gradually becomes thickened, and a black border is ultimately formed round it on the inside in continuity, at the umbilicus, with the coating of black varnish which covers the involute convexity or *anfractus* of the shell from the earliest stages. The septa, as seen in sections through the shell, become progressively thicker from the earliest to the latest, so that the last septum which precedes sexual maturity is, when completed, the thickest of all[1]. Another striking character which indicates the termination of the chamber-building activity of *Nautilus* is found in the fact that the last air-chamber of the finished shell is generally smaller than the one which preceded it, due no doubt to advancing age, but one of my bisected shells of *N. macromphalus* provides an apparent exception to this rule in that, though the black edge has been added to the lip of the shell, the final chamber is not smaller than the penultimate. It was formerly supposed that the most recent chamber was always, at its first formation, smaller than its predecessor, even in young growing shells, and this assumption was used as an argument in support of a theory of shell-growth by intussusception [Riefstahl], but it is not so, and the error has been duly corrected[2].

The total number of chambers constructed seems to vary considerably. Three shells of *N. pompilius* have 36, 34, and 33 chambers respectively, two of *N. macromphalus* have 28 and 27, one of *N. umbilicatus* 32.

Although the umbilicus of *N. pompilius* is closed externally by a deposit of callus it is well known that a section through the shell reveals the presence of an umbilical fossa in consequence of which the initial chamber of the shell has a free outer surface. In the middle of this surface when isolated by chipping away the rest of the shell there is a sub-rotund area with a slightly raised oval boss in the centre of it, and in the middle of the boss a shallow elongate depression, the whole somewhat resembling the structures known in plants as bordered pits. This is called after its discoverer as *Hyatt's scar*[3] and is the principal feature of the shell, concerning the nature of which and its relation to a possible protoconch we might expect to acquire special information from a study of the embryonic stages of development[4].

At the median dorsal border of the earlier septa, from the third to the twenty-second or thereabouts, there is a deep pit which occasions a prominent lobe to project backwards into the preceding chamber from each septum. This *dorsal lobe* of the septum was observed by Valenciennes and later writers, and an excellent illustration has been furnished more recently by Dr Appellöf[5].

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[1] This condition is not shown in many published figures of the shell, but is clearly reproduced in the collotype published by Dr R. von Lendenfeld in his "Bemerkung zu Riefstahl's Wachsthumstheorie der Cephalopoden-Schalen," *Zool. Jahrb. Syst.* III., 1888, pp. 317, 318, Taf. IX.

[2] Bather, F. A., "The Growth of Cephalopod Shells." *Geol. Mag.*, IV., pp. 446—449, 3 figg., 1887; also by the same author, "Professor Blake and Shell-growth in Cephalopoda." *Ann. Nat. Hist.*, June 1888, pp. 421—427; also same Journal for April, 1888, pp. 298—310. R. von Lendenfeld, *op. cit.*, 1888.

[3] Hyatt, A., "Fossil Cephalopods of the Museum of Comparative Zoölogy: Embryology." *Bull. Mus. Harvard*, III., pp. 59—111, Pl. III. fig. 1, 1883.

[4] Cf. Bather, F. A., "Cephalopod Beginnings." *Nat. Sci.*, V., 1894, pp. 422—436.

[5] Appellöf, A., "Die Schalen von *Sepia*, *Spirula* und *Nautilus*." *Svenska Ak. Handl.* XXV., Stockholm, 1893; see Taf. X. fig. 2.

The line of insertion of each septum into the wall of the shell is known as the *septal suture* and follows a broadly sinuous course, well indicated for example in a skiagraph made by Messrs J. Green and J. H. Gardiner and commented upon by Mr B. B. Woodward[1]. (Cf. Pl. LXXVII. fig. 1.)

In precise correspondence with the septal suture which bounds the fundus of the animal chamber (Wohnkammer) there is an aponeurotic band round the visceral portion of the mantle forming the boundary of the pallial area which secretes the septa (Pl. LXXV.). I figured this band in 1896, referring to it as the *septal contour*[2], and it has since been further illustrated by Mr L. E. Griffin[3] who speaks of it as the "posterior ventral aponeurotic band," having overlooked my previous account[4]. Recently, however, I have met with a still earlier description of this septal aponeurosis in the work of Appellöf (1893), though without illustration. Having referred to the *annulus* or horny girdle of Owen by which the visceral sac adheres to the shell all round its circumference between and including the shell-muscles, Appellöf (*op. cit.* p. 75) goes on to say:—"Hinter diesen [*i.e.* the annulus] und sehr deutlich markirt erstreckt sich rings um den Mantel eine zweite Linie, welche der Septalsutur anliegt. Dieselbe tritt durch ihre weissliche Farbe scharf hervor und scheint eine Verdickung im Mantel zu bilden."

The preceding remarks lead to the consideration of the method of formation of the septa. This is simple enough so far as the septum itself is concerned. What is not so easy to understand is the manner in which the animal glides bodily forwards in its shell so as to leave a space behind it which is destined to become the new air-chamber.

The foundation of a new septum consists of a very thin, easily torn membrane, presumably conchyolin, which appears as a cuticle over the entire septal area of the mantle, *i.e.* the area limited by the septal aponeurosis. Upon this membrane nacreous matter is deposited commencing from the septal suture, and the membrane itself remains as a thin pellicle over the hinder surface of the septum. This pellicle appears to better advantage in some specimens than in others. It is a striking circumstance, upon removing a young *Nautilus* from its shell, to find that the septum which constitutes the fundus of the animal chamber is composed of soft membrane only without any trace of nacreous substance. When a calcified septum is substituted for the primary membranous septum by the deposition of nacre, it is at first exceedingly thin and fragile, becoming gradually thickened by further secretion, but the size of the air-chamber is determined from the commencement of calcification and undergoes no subsequent change.

If the horny membrane which covers over the muscular impressions in the shell be removed, it will be found that each muscle-scar consists of a series of close-set concentric lines exactly like the growth-lines of the shell, not however continuous with the latter but quite independent, superposed upon the growth-lines of the shell, and traversing them at an angle. These superadded lines may be called the growth-lines of the muscles or briefly the *muscle-lines*, in contradistinction to the growth-lines of the shell, or simply, *shell-lines.* Careful inspection will further reveal the fact that what I have called the muscle-lines are not confined to the actual muscle-scar, they do not merely represent the symmetrical impressions of the muscle-fibres, but the concentric lines are continued behind the scar as far as the septal suture, thus clearly indicating a progressive forward movement of the muscles in correspondence with the growth of the entire animal.

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[1] *P. Malac. Soc. London*, II., 1896, p. 179, Pl. XV.

[2] Willey, A., "Letters from New Guinea." *Quart. J. Micr. Sc.*, Vol. 39, August 1896, p. 170, fig. 16 (see also below).

[3] Griffin, L. E., "Notes on the Anatomy of *Nautilus pompilius*." *Zool. Bull.* (Boston), Vol. I., 1897, p. 148, fig. 1.

[4] It is indicated without a description in a drawing by J. van der Hoeven, *Tr. Zool. Soc.*, IV., Part I., 1850.

It is important for a just appreciation of these details to note that the muscle-lines on the shell are concentric with the anterior border of the muscular impression, and have no relation to its posterior border, although the latter has a definite contour rendered visible in spite of the continuity of the muscle-lines across and behind it, by the fact that there is a glistening pearly sheen in the region of the muscular impression, and merely a dull lustre behind it, though it must be added that this distinction is more noticeable in some specimens than in others. (Pl. LXXVI. fig. 9.)

The nacreous deposit which overlies the shell-lines behind the anterior border of the muscular and annular impression, and is continued upon the face of the septum, has been interpreted as *hypostracum*, the rest of the pearly substance of the shell being the *ostracum*, while the external porcellanous pigmented layer is the *periostracum*[1].

Keferstein (1865) and Appellöf (1893) supposed that the mechanism of the forward movement of the muscles in the shell consisted of a resorption of muscular substance at the hinder border, coincident with a formation of fresh muscular substance in front. But this pretended resorption of muscle-fibres could not be confined to the ends of the muscles where they abut upon the shell, but must affect the entire body of the muscles. There is no evidence whatever that anything of the kind takes place since the muscles increase in size *pari passu* with the growth of the animal, and the presence of the concentric muscle-lines on the shell, visible as they are from the septal suture to the anterior border of the muscle-scar on each side, is clearly indicative of a very gradual forward gliding of the animal. As the animal grows it must of necessity move forwards within the rigid walls of the shell, since the increase in size takes place in every direction, quite as much in girth as in length. At the same time the soft visceral sac can accommodate itself to a certain extent to straitened circumstances, sufficiently to avoid any sudden catastrophic movement, and meanwhile gas is secreted by or through the thin *septal area* of the mantle, and when the limit of growth at any particular period is reached, a new septum is laid down in the manner which I have described above. As the animal moves forward over a tract equivalent to the interval between two successive septa, a calcareous deposit is formed between the old and the new septal sutures.

With regard to the relation subsisting between the septal aponeurosis and the annulus, or to keep uniformity of nomenclature, the annular aponeurosis[2] which secretes the horny girdle on its surface, it is to be noted that, on the dorsal side of the mantle these structures are more or less confounded together, while ventrally there is in adult specimens a wide interval between them, and in the centre of this intervening pallial tract may be seen the line of insertion of what Huxley[1] named the *pallio-visceral ligament*, that is, the membrane with the three fontanelles which incompletely divides the pericardial from the visceral portion of the coelom. In young examples the interval between the septal and annular bands is both relatively and absolutely much less considerable. These relations also leave their impress on the shell.

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[1] Thiele, J., "Beiträge zur Kenntnis der Mollusken. II. Über die Molluskenschale." *Zeitschr. wiss. Zool.*, Bd. 55, 1893, see p. 234 with text-figure. In the figure the author has omitted to represent the posterior contour of the actual muscular impression.

[2] Valenciennes likened the annulus to an aponeurosis.

The occurrence of *muscle-lines* on the shell-wall behind the posterior border of the actual muscle-scar, to which I have alluded above, seems to me to be specially worthy of note as indicating gradual normal growth. So true is this that if the horny membrane is lost, especially in young shells, it is sometimes not easy to discern the posterior limits of the muscular impressions, and Appellöf (1893) states that in several small dried shells of *N. pompilius* he has sought in vain for an indication of the muscle-scar and annulus.

The above description of the growth of *Nautilus* is in substantial accord with the observations of Keferstein (1865), except with regard to his and Appellöf's hypothesis of a local resorption of muscular tissue. So far as I can ascertain, my record of the fact that the hard nacreous calcified septum is actually preceded by a soft membranous septum is new.

The three facts which are necessary to remember when attempting to form a subjective conception of the mode of growth of *Nautilus* are as follows:—

(1) Growth in bulk of the animal taking place at regular intervals, terminated respectively by the formation of a new septum.

(2) Rigidity of the shell necessitating a forward movement of the too bulky animal.

(3) Faculty of secreting gas.

A few words remain to be said concerning the anterior free pallial fold and the nuchal membrane. The free border of the mantle forms a continuous collar round the entire periphery of the animal, and may be considered in three divisions, ventro-lateral, umbilical, and dorsal. The contour of the mantle-edge accurately corresponds with that of the mouth of the shell, and the mantle is never reflected upon the external surface of the shell, except in the region of the involute convexity (*anfractus*). By a coincidence it happens that in the recent species of *Nautilus* the contour of the lip of the shell is a close repetition, on an enlarged scale and in a different plane, of the shape of the septal suture.

The *dorsal fold* of the mantle was described and named by Owen but not correctly figured by him, a better illustration being furnished by Van der Hoeven in 1850 in the *Transactions* of the Zoological Society. It is reflected over the involute convexity of the shell and apparently secretes the layer of black varnish which distinguishes this part, so that the sharp line with which this layer terminates denotes the extent to which the mantle may be reflected over this portion of the shell. I received the impression that the dorsal fold of the mantle does not always cover the black area but may be retracted so that the nuchal membrane which adheres to the hinder concavity of the hood comes to play upon this smooth surface. Frequently the animal executes violent up-and-down movements in the shell, and at such times my observation led me to believe that it was the nuchal membrane which plied against the black surface, and I even thought that this membrane was responsible for the black deposit[1]. But the evidence of sections which I have since made is against this view, and I now think that the older writers who inferred that the black pigment was secreted by the dorsal fold of the mantle, and Professor Joubin[2] who described the gland-cells in section, are right. The epidermal cells on the outer side of the dorsal fold of the mantle are obviously glandular and more columnar than those on the inner surface, whereas the epidermis of the nuchal membrane is of the nature of a mucous membrane and is lower on the side which is next to the shell than on the obverse side. I have often seen the mantle being withdrawn from the upper portion of the convexity of the shell when I have been handling living *Nautili*, but I am unable to state the precise conditions under which the dorsal fold of the mantle and the nuchal membrane respectively come into contact with the black area. There are moreover distinct indications in the structure of the shell itself showing that the mantle is not always under normal conditions kept stretched over the entire black area, since there is another *margo limitans* situated at about one-third of the distance between the dorsal border of the septal suture and the *margo limitans* of the black area. The second line to which I refer represents the limit of a thin nacreous deposit which is laid over the black deposit on that part of the involute convexity or *anfractus* (Van der Hoeven) of the shell which faces downwards when the shell is held with the mouth directed upwards. (Pl. LXXVII. fig. 1.)

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[1] Huxley, T. H., "On some points in the anatomy of *Nautilus pompilius*." *J. Linn. Soc.*, III. 1859, pp. 36—44.

The facts may be summarised by saying that the free lip of the shell constitutes the *margo limitans* of the ventro-lateral fold of the mantle, while the *anfractus* presents two *margines limitantes* of the dorsal pallial fold, namely, the limit of the nacreous deposit and the limit of the black varnish. In quite small shells 33 mm. in diameter, measured in section from the anterior lip to the convex posterior surface (the line of maximum diameter passing some distance below the umbilicus), the nacreous deposit extends halfway over the black area; in older and in adult shells it occupies no more than one-third of the black area.

The dorsal fold of the mantle has therefore two functions to perform, the deposition of black varnish over the whole of the *anfractus* (involute convexity) and of nacre upon the lower portion only.

With regard to the topographical relations of the nuchal membrane I can only call to mind one complete and accurate account of it, namely, that given by Professor Lankester in the article "Mollusca" (*Encyc. Brit.*, 9th edit., 1883). Owen (1832, p. 12) correctly describes its position and shape as a "semilunar ridge," but adds that "it is from this ridge that the mantle is immediately continued to form the concave [dorsal] fold." Van der Hoeven (1850) while adding a new fact repeats Owen's mistake as to a direct connection between the nuchal membrane and the dorsal fold of the mantle in these words:—"Under that fold [the dorsal fold] is a smaller plate of nearly the same form but adherent to the posterior declivous surface of the hood and only free at its circumference. This plate is of an aponeurotic texture and a white colour: *at both sides it is united to the dorsal fold* [italics mine] and below it seems to have an intimate connection with the two side parts of the funnel, and indeed to be a continuation of those parts." The new fact signalised by Van der Hoeven is the relation of the nuchal membrane to the *alae infundibuli* into which alone it passes behind and below (Pl. LXXVII. fig. 4).

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[1] Willey, A., "Letters on Nautilus, 1896." *Quart. J. Micr. Sc.*, Vol. 39, p. 172.

[2] Joubin, L., "Recherches sur la coloration du tégument chez les Céphalopodes, 4^me^ partie, Glande sécrétant le vernis noir chez le Nautile." *Arch. zool. expér.* (2) x., 1892, pp. 319—324.

The umbilical portion of the pallial border is the angle which unites the dorsal and ventro-lateral folds together, and in *N. pompilius* secretes the callus which conceals the true umbilicus of the shell.

6. Ventral Pallial Complex.

In order to render my description of the pallial topography relatively complete it is desirable to devote a special section to an enumeration of the organs which are contained in the spacious mantle-cavity[1] produced by the deep ventro-lateral fold of the mantle. The insertion of this fold into the body-wall is not so easily understood as in the case of the dorsal fold as it involves some of the organs, notably the branchiae, osphradia, anus and renal organs, which in other Cephalopods form part of the body proper and are not carried up into and upon the mantle itself.

The various organs, lines and regions which compose the ventral pallial complex are mapped out in the coloured figure on Plate LXXV. which shows their exact normal positions in the fresh condition as seen upon and through the thin pallial wall. Such a figure as that referred to is serviceable from the point of view of topographical anatomy on account of the degree of transparency possessed by the living mantle as compared with its opacity in preserved specimens.

The mantle commences as a free fold behind the renal sacs, so that these structures actually penetrate into the substance of the mantle, and their apertures as well as the viscero-pericardial apertures open upon the inner surface of the mantle. The pallial insertion of the above-named organs and also of the nidamental gland in the female, by all of which *Nautilus* differs from the Dibranchs, has doubtless been noted by anatomists who have dissected this animal, and has further received special attention from Dr L. E. Griffin[2], who points out that "there is in the *Nautilus pompilius* the same arrangement of the parts of the pallial complex as in many Gasteropoda." It may be noted here that the particular Gasteropoda to which *Nautilus*, in common with other Cephalopoda, is specially comparable, are the Zygobranchiate Prosobranchiata which include *Haliotis* and *Pleurotomaria*[3].

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[1] Branchial cavity of Vrolik, sub-pallial chamber of Lankester.

[2] Griffin, L. E., "Notes on the Anatomy of *Nautilus pompilius*." *Zool. Bull.* (Boston), Vol. I., 1897. Section headed "The Pallial Complex" on p. 153.

[3] For *Haliotis* see Wegmann, H., "Contributions à l'histoire naturelle des Haliotides." *Arch. zool. expér.* (2) II., 1884, pp. 289—379, Pls. XV.—XIX. For *Pleurotomaria* the work of the lamented Martin F. Woodward should be consulted, "The Anatomy of *Pleurotomaria beyrichii* Hilg." *Quart. J. Micr. Sc.*, Vol. 44, March 1901, pp. 215—268.

In comparing *Nautilus* with the dibranchiate Cephalopods Professor Lankester (1883, *Encyc. Brit.*) points out that "in the former the base of the fold forming the mantle-skirt comprises in its area a part of what is unreflected visceral hump in the latter."

The consequence of this invasion of organs into the substance of the mantle is that when the ventro-lateral fold of the latter is pulled back and turned inside out in order to expose the pallial organs, the normal antero-posterior relations of parts are inverted and what is actually placed anteriorly in the natural position of the mantle (Pl. LXXV.) becomes posterior when the mantle is retroverted (Pl. LXXVI.). This simple fact has led to much confusion of terminology, actual topographical conditions being confused either with mechanically retroverted positions or with inferred morphological relations of parts[1].

Of the nine apertures which open into or near the fundus of the mantle-cavity only four were seen by Owen, namely the two viscero-pericardial orifices, the anus and the opening of the female generative apparatus. Four more, the renal apertures, were added by Valenciennes (1841), and their relations further elucidated by Vrolik[2]. The full number of nine was first established in 1883 by the important discovery announced by Lankester and Bourne[3] of the existence of a rudimentary antimere of the functional generative orifice, represented on the left side by the external pore of the vestigial structure known as the *pyriform gland.*

In the male the generative pore is carried forwards and occupies a prominent median position adherent to the *vena cava,* but the penis is divided by a septum internally so that it possesses two lumina. Externally the terminal portion of the male generative apparatus appears to be symmetrical, an appearance which is heightened especially in the young by the existence of an arcuate radix on the left side as well as that which leads to the so-called Needhamian vesicle on the right, but the left lumen ends blindly behind and as shown by Lankester, Bourne, and later by Graham Kerr[4], the opening of the pyriform gland is independent and has the same relations in the male as in the female.

In the female the genital orifice is placed on the right side precisely in the angle made by the insertion of the mantle into the body-wall, and is represented by a transverse bilabiate vulva which is prominent in the adult but lies deep and concealed in the young.

7. SIPHUNCLE AND PALLIAL VESSELS.

It may seem strange to unite these structures in one heading but it is not so strange as it looks, especially when we remember that the siphuncle is essentially and entirely an appendix of the visceral sac, that is to say, of the visceral portion of the mantle, and that it owes whatever physiological importance it may possess to the blood which is supplied to it from the pallial circulation. While describing the latter we are necessarily led to speak of the siphuncle, which is a vascular vermiform process of the mantle and hence the reason for their association in one chapter.

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[1] This point will be incidentally referred to in subsequent sections of this essay.

[2] Vrolik, W., (*a*) "Brief aan J. J. Rochussen over het ontleedkundig zamenstel van den *Nautilus pompilius.*" *Tijdschr. natuurk. Wet.* (Netherlands), II. 1849, pp. 307—327, 2 plates. (*b*) "Lettre sur quelques points de l'organisation de l'animal du Nautile flambé." *Mém. Soc. Normandie*, X., 1855, 16 pp., 2 plates.

[3] Lankester, E. R. and Bourne, A. G., "On the existence of Spengel's olfactory organ and of paired genital ducts in the Pearly Nautilus." *Quart. J. Micr. Sc.*, Vol. 23, 1883, pp. 340—348.

[4] Kerr, J. G., "On some points in the anatomy of *Nautilus pompilius.*" *P. Zool. Soc. London*, 1895, pp. 664—686; see p. 672, fig. 3 and Pl. XXXIX. fig. 1.

By means of injections practised upon fresh specimens when I was living on the shores of Blanche Bay, I obtained a fair knowledge of the distribution of the pallial arteries, such in fact as had not been possible to my predecessors working with preserved material only. I published an account of the results of my injections in 1896 (*Quart. Journ. Micr. Sc.*, Vol. 39), which I propose to recapitulate here, the more important, in my own opinion, relating to the vascularisation of the siphuncle, which does not, as was formerly supposed from the time of Owen's memoir (1832) to that of Dr Haller's memoir[1], published in 1895, receive a main artery direct from the heart but merely a secondary and two or three tertiary ramifications from the *posterior pallial artery*.

Looked at from below through the transparent wall of the mantle the heart is seen lying in the pericardium in the form of a transversely elongated somewhat oblong body placed immediately behind the level of the mantle-insertion and receiving at its four corners the paired branchio-cardiac or efferent branchial vessels (Pl. LXXXII.). The hinder surface of the heart is slightly convex, while the anterior surface is emarginate, and from the base of the groove there issues a very short vessel called by Owen the "lesser aorta," which he correctly described as dividing almost immediately into two branches, of which he thought the anterior was "exclusively distributed to the mucous organ of the oviduct" (1832, p. 36), by which he meant the nidamental gland, while the posterior passing backwards between the ovary and the gizzard entered, "without diminution of size, the membranous tube that traverses the partitions of the shell." A third branch (intestinal artery) arising after the bifurcation of the lesser aorta was correctly described by Owen as being distributed to the mesentery between the ascending and descending limbs of the last loop of the intestine.

The two primary branches of the lesser aorta are respectively the anterior and posterior pallial arteries, the former supplying the anterior free mantle fold with arterial blood, and the latter irrigating the posterior or visceral portion of the mantle, including the siphuncle.

The anterior pallial artery bends at first inwards and downwards to the middle line, and then runs forwards below the skin at the surface of the renal sacs. At the point where it turns forwards a small intestinal branch (*i.a.*) is given off. Arrived at the anterior limit of the region of the renal sacs, which, as already mentioned, forms part of the free mantle-skirt, the anterior pallial artery passes into the substance of the mantle and runs forwards towards the free margin of the latter. At some distance, 13 or 14 mm., from the free margin of the mantle, the anterior pallial artery divides into two main submarginal arteries (*m. a.*) from which numerous radial arteries (*r. a.*) proceed to the mantle-edge.

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[1] Haller, B., "Beiträge zur Kenntniss der Morphologie von *Nautilus pompilius*" in Semon's *Zool. Forschungsreisen in Australien und dem Malayischen Archipel.*, Bd. v., Lief. II. 1895, see p. 200, and Taf. XI. fig. 2.

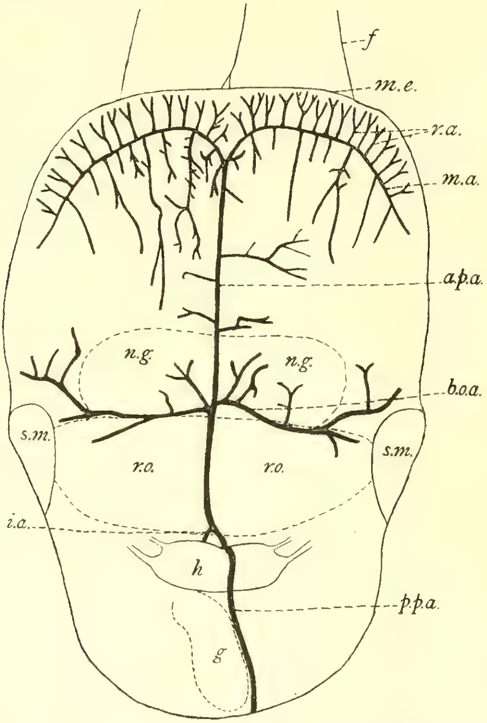
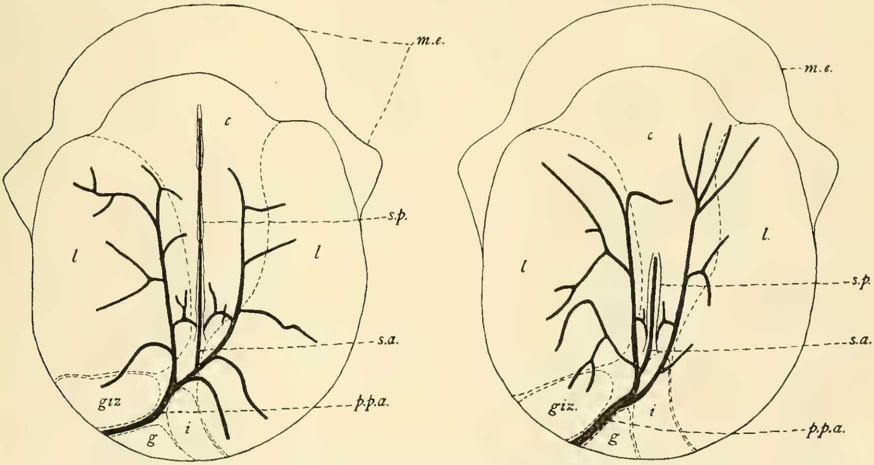


FIG. 3. *N. pompilius*, ♀. View of ventral surface of pallial and visceral regions, to show the course of the pallial arteries; *f.* funnel; *m.e.* free edge of mantle; *r.a.* radial pallial arteries; *m.a.* marginal pallial artery; *a.p.a.* anterior pallial artery; *n.g.* region of nidamental gland; *b.o.a.* branchio-osphradial artery; *s.m.* shell-muscle; *r.o.* region of renal organs; *h.* heart; *p.p.a.* posterior pallial artery; *g.* gonad; *i.a.* intestinal branch of anterior pallial artery. [From *Quart. J. Micr. Sc.* Vol. 39, 1896.]

Exactly at the point where the anterior pallial artery passes into the substance of the mantle, that is to say at the level of the anterior limit of the renal region, a pair of lateral branches arise almost at right angles to the main vessel. I suggested the name *branchio-osphradial* for these arteries (*b.o.a.*) since among their minor ramifications they send branches up to the tips of the branchiae supplying the integument of the latter, and also a small branch into each of the four osphradia. In the female they also supply the nidamental gland. The branchial branches of these arteries are of the nature of arterioles or intrinsic arteries of the gills in their capacity of fleshy organs.

The posterior pallial artery runs backwards, crossing over the ventral surface of the heart and leaving the pericardium through the median orifice of the pallio-visceral ligament. It then passes backwards without branching on the left side of the gonad between the latter and the gizzard, adhering to the gonad by a ligament named by Haller the *genito-intestinal ligament.* This ligament binds the gonad and intestine to the posterior wall of the perivisceral coelom with an insertion into the wall of some 20 mm. in length running in a dorso-ventral direction. At a site near the middle of the line of insertion of the genito-intestinal ligament into the posterior body-wall occurs the root of the siphuncle. The posterior pallial artery reaches the posterior body-wall through the intermediation of the free ventral border of the ligament at a point distant by 5 mm. from the root of the siphuncle. Upon reaching, in the way described above, what is approximately the middle point of the posterior rounded surface of the body, the posterior pallial artery passes into the integument and immediately divides into two main branches which supply the dorsal and posterior regions of the mantle, including the siphuncle. The two main branches of the posterior pallial artery are the *pallio-septal* arteries, so called because they supply that portion of the mantle which secretes the septa of the shell.



Figs. 4 and 5. *N. pompilius*, ♂. Two views of the dorsal surface of the pallio-visceral region, to show the principal ramifications of the posterior pallial artery. The siphuncular artery (*s.a.*) has a dextral origin in Fig. 4, sinistral in Fig. 5.

Other letters:—*m.e.* free edge of the dorsal and umbilical folds of the mantle; *c.* region of crop; *s.p.* siphuncle; *l.* region of liver; *p.p.a.* posterior pallial artery; *giz.* region of stomach; *g.* region of gonad; *i.* region of intestine. [From *Quart. J. Micr. Sc.* Vol. 39, 1896.]

A variable number of small arteries are distributed to the siphuncle, but there is one branch, a secondary branch of the posterior pallial artery, which may be regarded essentially as the *siphuncular artery.* This arises indifferently from either the right or the left of the two principal branches. Owen (1832), Valenciennes (1841), Vrolik (1855), and Haller (1895) have described what I have called the posterior pallial artery as passing direct to the siphuncle. Keferstein (1865) with more accuracy said that it passes "nach hinten zur Körperhaut und besonders zum Sipho." Injections show that the siphuncular artery is simply on a par with the other ramifications of the posterior pallial artery, the ultimate branches of which constitute a remarkably rich system of irrigation for the septum-producing area of the mantle.

Before continuing my account of the pallial arteries it will be convenient at this point to complete what I have to say regarding the connections of the siphuncle. Owen, as I have already mentioned above, described a direct communication between the pericardial cavity and the siphuncle, saying (memoir, p. 27):—"by the side of this vessel" [the posterior pallial artery] "a free passage is continued between the gizzard and ovary into the membranous tube or siphon that traverses the divisions of the shell; thus establishing a communication between the interior of that tube and the exterior of the animal" [through the viscero-pericardial apertures].

Valenciennes (1841) denied any communication between the siphuncle and the exterior through the mediation of the pericardium, and further affirmed that it did not even open into the abdominal cavity at its base. Vrolik (1855, p. 7) said that Valenciennes was wrong, "car, d'après ce que j'ai vu, le siphon s'ouvre dans la cavité abdominale, comme la pl. I., fig. 5c le démontre." But on turning to the figure referred to we find that it is by no means demonstrative in this respect. Vrolik was confident as to the actuality of his observations, and stated in a foot-note that he had shown his preparation to many foreign anatomists, including Kölliker, who mentioned it among the impressions of his travels in his *Zeitschrift.* It is no light matter to attribute an error to an anatomist of Vrolik's reputation, especially since he alludes at another part of the "Lettre" from which I am quoting to "l'erreur grossière de voir des ouvertures là où elles ne sont pas." Nevertheless I shall proceed to show that he was wrong in this matter in spite of the asseverations of Keferstein (1865) and Haller (1895). Keferstein[1] defines the siphuncle in these words:—"Der Sipho ist hinten eine röhrige Fortsetzung der Körperhöhle, wird der ganzen Länge nach von einer Arterie durchlaufen und muss grade wie die Intervisceralräume des Körpersackes venöses Blut enthalten können."

It is true that in addition to its main artery, the siphuncle is traversed by a wide axial cavity, and it is perhaps to be inferred from Keferstein's definition that this axial cavity of the siphuncle is a continuation of the abdominal or perivisceral cavity in which the gonad and other viscera lie, in other words that it is part of the secondary body-cavity or coelom. But whatever inference may be drawn from somewhat vague statements, we find precise assurances on this subject in the recent memoir of Dr Haller (1895, p. 201), who says:—"Der Sipho communicirt direct mit dem grossen Cölomraum, und zwar, da sich über ihrer Mündung der ventrale Theil des Genitointestinal-ligamentes an die hintere Wand des Cöloms befestigt, scheinbar mit zwei Oeffnungen, thatsachlich aber nur mit einer. Somit ist das Innere vom Sipho als die directe Fortsetzung des grossen Cölomraumes aufzufassen, und das Cölomepithel setzt sich als ein niedrig-cubisches, beinahe plattes Epithel in die Siphonalhöhlung continuirlich fort."

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[1] *Nachr. Ges. Göttingen* 1865, p. 369.

The relative importance of a correct knowledge of the nature of the siphuncular cavity is too obvious to render an apology for the quotations which I have given necessary. In fact this cavity is a venous cavity or haemocoel, as I have satisfied myself by means of transverse and longitudinal sections, but above all by dissection, which besides showing the non-existence of any opening into the coelom has revealed the presence of a hitherto undescribed venous channel, which I will call the *posterior pallial vein,* into which the *siphuncular vein, i.e.* the axial cavity of the siphuncle, discharges (Pl. LXXVI., figs. 7 and 8). It is quite probable that the posterior pallial vein which runs above, approximated to, and parallel with, the posterior pallial artery in the genito-intestinal ligament, is identical with the "free passage" which Owen described as coursing alongside of the posterior pallial artery between the pericardium and the siphuncle. As a matter of fact the channel which occurs in this position is a vein which runs forwards until it arrives at the pericardium, when it bends up above the dorsal wall of the latter and enters the central venous sinus from whence the afferent branchial vessels are given off.

The finer structure of the siphuncle (Pl. LXXXIII.) is complicated and not readily intelligible. Surrounding the central vein is a loose meshwork of trabeculae, the meshes communicating with one another and with the central vein. The communications between the peripheral system of spaces and the central sinus are best seen in longitudinal sections, but are also to be found in transverse sections. The external epithelium of the true or pallial siphuncle which secretes the partially calcified and partially horny siphuncle, which remains behind after the soft parts are extracted, presents a very peculiar structure. This has been in part correctly described by Haller, who states (*op. cit.*, p. 201) that the entire surface of the siphuncle is thrown into very fine longitudinal folds due to the plaited *membrana basilaris* of the epithelium, and in each plication of the basement-membrane there is a narrow space lined by flattened endothelium (Haller, *op. cit.*, Taf. XII., fig. 19).

I can confirm the existence of these folds, although they do not appear in my preparations to be so regular as Dr Haller describes and figures them. Moreover I cannot see the regular deep epidermal pits which alternate in correspondence with the subjacent mesodermal folds in his figures. What seems very remarkable is the fact that the spaces in the folds are in reality prolongations from the meshes of the trabecular tissue of the siphuncle, and therefore represent *intra-epidermal blood-spaces.* I think this circumstance must throw some light on the function of the siphuncle, which is essentially a vascular appendix. I have already expressed the possibility that the siphuncle would be capable of keeping the air in the chambers up to the normal pressure by making good losses caused by diffusion. The same, or a closely similar suggestion, was in fact made by Keferstein (1865, *op. cit.* p. 374)[1].

Coupling the existence of intra-epidermal venous spaces with my observation recorded above, of the automatic injection of the pallial veins with gas (Pl. LXXXII.), it seems that the conclusion may be drawn that the separation of gas rich in nitrogen is a special property of the venous system of *Nautilus*. Whether this supposition will prove to be sound or not, the observations are sufficiently singular to merit the attention of future investigators.

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[1] Cf. Meigen, W., "Ueber den hydrostatischen Apparat des *Nautilus pompilius.*" *Arch. Naturg.* 36 Jhg. Bd. I. 1870, pp. 1—34. This author confirms Keferstein's theory.

The spongy trabecular tissue of the siphuncle becomes looser, *i.e.* the meshes become larger near the root of the siphuncle, and where the latter abuts upon the body-wall there is generally to be seen from the inside of the perivisceral coelom a large cushion, divided superficially into two equal or nearly equal portions, by the insertion of the genito-intestinal ligament. In certain conditions of preservation the wall of this sac is very easily ruptured, so as to produce the appearance of a natural orifice, although such is not and cannot be present, since the cavity of the sac is the radical sinus of the siphuncular vein, and opens directly into the posterior pallial vein. When the sac is cut open it is found to contain a flocculent substance, composed partly of blood, and partly of the trabeculae described above.

The radical sinus of the siphuncle of *Nautilus* is obviously identical in principle with the *pallio-siphonal sinus* described by Huxley and Pelseneer[1] in their joint work on *Spirula*. In *Spirula* we are told that the cavity of the membranous siphuncle is a blood sinus which opens at the root of the siphuncle into a relatively large space, which is the pallio-siphonal sinus. The irrefutable demonstration of the existence of corresponding connections in *Nautilus* seems to me to be a matter of uncommon interest.

The peculiar segmentation of the siphuncle due to shallow constrictions at the points where it traverses the septa was first observed by Valenciennes. According to Appellöf (*op. cit.* 1893, p. 79 *et seq.*), it is open to question how far back the living siphuncle extends in the adult shell, and it is even quite certain that it does not extend into the first chamber, since he has been able to confirm Hyatt's statement "dass auch der Sifo der zweiten Kammer wirklich......... blind geschlossen ist." In extracting the animal from the shell, varying lengths of the siphuncle emerge. I cannot assert that I have ever obtained a complete siphuncle, but often one with upwards of twenty segments.

I made some experimental observations on *Nautili* with severed siphuncle for the purpose of ascertaining whether this organ performed a definite immediate function. The result, so far as it went, seemed to indicate that the cutting of the siphuncle does not temporarily affect the vitality of the animal, does not inhibit movements of translation and does not prevent it from floating at the surface, nor from sinking to the bottom. Its function must therefore be a cumulative one, a conclusion in accord with the suggestion that it may serve to keep the air-chambers at the proper tension. I found that the best way of performing the operation was to saw through the shell in the neighbourhood of the posterior portion of the body of the animal over the cardiac region. If the shell with the living animal inside be held mouth downwards, the cardiac region lies approximately in the same vertical transverse plane with the points at which the free lip of the shell merges into the umbilicus. When a large enough hole has been made in the shell to admit the scissors, the shell being still held upside down, the postero-ventral visceral portion of the body behind the annulus usually detaches itself from the shell, or can be readily caused to do so, and sinking inwards, exposes the root of the siphuncle, which can then be severed. Upon righting the shell the body resumes its normal contact with the fundus of the shell, thus preventing an immediate and extensive hemorrhage. For example a *Nautilus* treated in this way, and replaced in the sea at a suitable spot, swam about vigorously for some time in the middle stratum of water, but chiefly at a little distance from the bottom. Others remained floating and swimming about on the surface during the whole time of observation. They did not

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[1] Huxley, Rt. Hon. T. H., and Pelseneer, P., "Report on the specimen of the genus *Spirula* collected by H.M.S. Challenger." Published as the 83rd and last part of the Zoological Series of Challenger Reports, and inserted as an Appendix to the Summary of Results, second part, 1895. Plates by Huxley, text by Pelseneer. For the account of the pallio-siphonal sinus see p. 24, text-fig. Q.

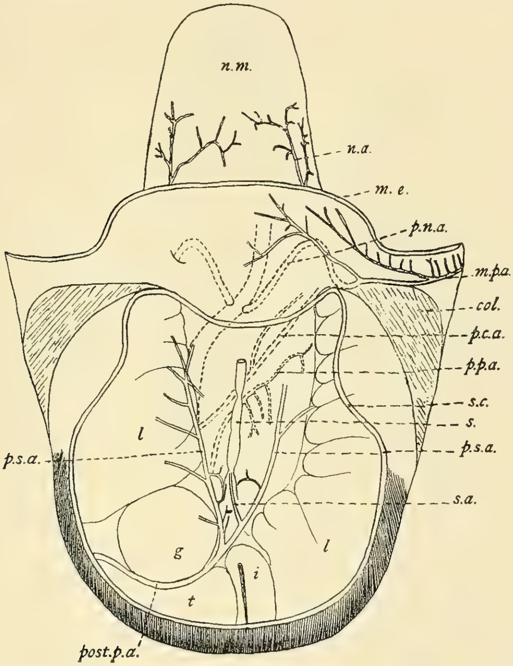

Fig. 6. *N. pompilius*, ♂. Dorso-posterior aspect of visceral region, to illustrate the circulus pallialis and the septal contour; *n.m.* nuchal membrane; *n.a.* nuchal artery; *m.e.* free mantle-edge; *p.n.a.* pallio-nuchal artery; *m.p.a.* marginal pallial artery; *col.* columellar or shell muscle; *p.c.a.* posterior columellar artery; *p.p.a.* posterior proventricular artery; *s.c.* septal contour; *s.* siphuncle; *p.s.a.* pallio-septal arteries; *s.a.* siphuncular artery; *l.* liver; *i.* intestine; *t.* testis; *post.p.a.* posterior pallial artery; *g.* gizzard.

N.B.—The dorsal aorta and its branches are indicated by dotted lines. They show dimly through the skin when injected. [From *Quart. J. Micr. Sc.* Vol. 39, 1896.]

go far in one direction, but tended to move in circles, as they sometimes do without severance of the siphuncle. If one of the individuals floating at the surface was forced down to the bottom with a hand-net it would slowly rise to the surface again, as also often happens with a *Nautilus* which has not been operated upon. Another specimen showed the opposite tendency to sink to the bottom very gradually.

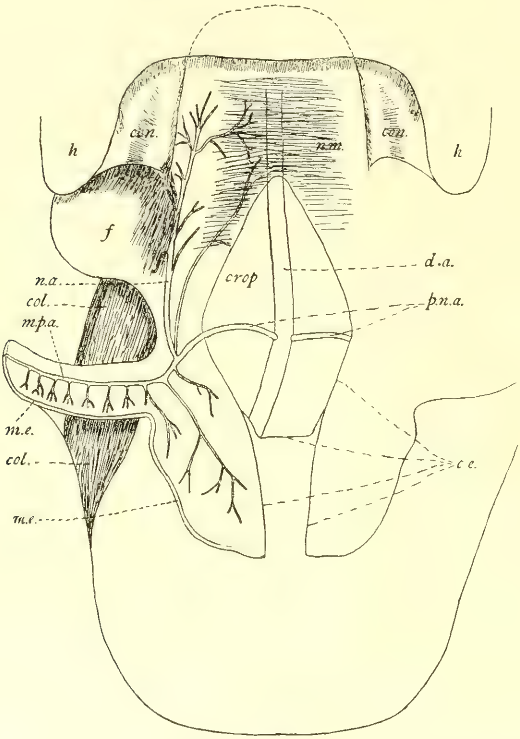

Fig. 7. *N. pompilius*, ♂. View of nuchal region, to further illustrate the circulus pallialis. The dorsal free mantle-edge is reflected and a median incision made. *h.* hood; *con.* concavity at base of hood, in which the nuchal membrane (*n.m.*) lies; *f.* dorso-posterior portion of funnel; *n.a.* nuchal artery; *col.* columellar muscle; *m.p.a.* marginal pallial artery; *p.n.a.* pallio-nuchal arteries; *d.a.* dorsal aorta; *m.e.* free mantle edge; *c.e.* cut edges of mantle and body-wall.

N.B.—The dorsal aorta shapes its course in this region in accordance with the state of repletion of the crop. [From *Quart. J. Micr. Sc.* Vol. 39, 1896.]

Some further features in the pallial circulation of *Nautilus* still remain to be described before concluding this chapter. After successful injections a striking peculiarity in connection with the anterior pallial artery may be observed. It will be remembered that upon approaching the mantle border in the mid-ventral line, this artery bifurcates into two submarginal arteries (*m.p.a.*).

The submarginal pallial artery is continued dorsally on each side into a branch of the systemic or greater aorta, so that a complete arterial circuit, the *circulus pallialis*, is achieved. I have even partially injected the pallial arteries from the dorsal aorta itself, although naturally the fluid did not proceed very far in the centripetal direction. Thus by means of the submarginal arteries the system of the lesser aorta becomes confluent with that of the greater aorta, or in other words, there is an anastomosis between the pallial circulation and the systemic circulation.

In one of the figures here reproduced the union of the submarginal arteries with the dorsal aorta is represented as seen through the mantle; in the other it is shown after the mantle has been slit open and turned back, and a further incision made into the body-wall in the nuchal region. The vessel which effects the junction is called the *pallio-nuchal artery* (*p.n.a.*). The actual point where the confluence takes place corresponds with the umbilical region of the mantle, and with the angle of insertion of the mantle in this region into the body-wall.

From the angles formed by the confluence of the pallio-nuchal with the submarginal arteries a branch is distributed forwards to the nuchal membrane. (Fig. 7.)

Finally I have to record some observations in the pallial veins. Under ordinary circumstances one might never suspect the occurrence of definite venous channels in the mantle. When a *Nautilus* kept in a confined space becomes moribund, it usually rises to the surface, owing apparently to an abundant production of gas in the interior of the body. If it be allowed to die and be then removed from the shell the veins are found to be injected with gas, most likely due to a regurgitation of gas, if the expression may be allowed, through the siphuncular venous sinus and posterior pallial vein, into the general venous or lacunar system of the body. Under these conditions the finest ramifications of the veins, especially in the free mantle-flap, are displayed with a clearness which could hardly be attained, certainly not surpassed by artificial injection. The mantle in fact is seen to be riddled by these veins, which are collected into two main channels, placed on either side of the anterior pallial artery, and discharging behind into the afferent branchial vessels. At the sides of the mantle there may be seen a number of lateral pallial veins, which appear to open into a large sinus situated over the shell muscle. (Pl. LXXXII.)

8. Funnel and Capito-pedal Cartilage.

It is a fact of some interest which deserves to be brought into relief, that the cartilaginous endoskeleton of *Nautilus* essentially belongs to the funnel, it is the *sustentaculum infundibuli* besides serving incidentally as the foundation and support of the entire cephalopodium, and affording a fulcrum for the insertion of all the principal muscles of the body. It agrees analogically in point of form with the hyoid cartilage of Vertebrates and the nuchal chondroid skeleton of Enteropneusta, consisting as it does of a median body with anterior and posterior cornua, the whole being shaped somewhat like the letter H. It has frequently been designated by the same term which is applied to the principal cartilage of the Dibranchs, namely, *cephalic cartilage*[1], but this name as applied to the cartilage of the Tetrabranchs is not only a misnomer but is positively misleading, since the cephalic cartilage of the former is a *cranial cartilage* having essential topographical relations with the central nervous system, and presenting definite fossae for the reception of the cerebral, pedal and visceral ganglionic centres, and for the protection of the otocysts, and foramina for the exits of nerves.

In *Nautilus* the arrangement is more primitive in so far that the cartilage has essential relations with the motor system generally (funnel and musculature), and merely exhibits incidental contiguity with regard to the more ventrally situated parts of the nervous and sensory systems. It surrounds no part of the last-named systems, is not perforated by any nerves, and is only traversed by one pair of blood-vessels, namely, the *infundibular arteries* (Pl. LXXXI.). The principal fossae which it presents are related to parts of the venous system, *e.g.* there is a deep fossa on each side nearly enclosed by cartilage, for the passage of the *infundibular vein*, and a spacious median fossa for the anterior reservoir of the *vena cava*. The deep fossa described by Owen for the lodgment of the optic ganglia has no existence.

The anterior cornua of the cartilage of *Nautilus* extend forwards into the substance of the funnel[2], which they help to keep open just as the posterior cornua of the skeleton in Enteropneusta keep the mouth open; the posterior cornua occupy the raphe which separates the *siphonopodium* (funnel) from the *cephalopodium*; finally the body of the skeleton lies at or near the angle of insertion of the funnel into the body-wall.

The ventral surface of the body of the cartilage is produced into a median keel which serves for the insertion of the transverse muscles at the base of the funnel, and its upper surface is complicated by its special relation to the important venous sinus, which collects the blood from the head and funnel and passes it on to the *vena cava*. This sinus may conveniently be termed the *endochondral sinus*[3].

After what has been said it will be evident that the term "capito-pedal" introduced by Professor Lankester[4], describes the cartilage of *Nautilus* more appropriately than any other available expression. Nevertheless the cartilage undoubtedly affords some support and protection to the ganglionic complex and otocyst, especially the latter, since conjunctive trabeculae traverse the space between the perineurium and the perichondrium, and also between the periotic membrane and the latter, in fact the loculus in which the otocyst lies is bounded posteriorly by the perichondrium and anteriorly by the brachial or pedal perineurium.

The direction of the long axis of the cartilaginous skeleton of *Nautilus* is probably of importance in regard to the more general question of Cephalopod orientation, and it may be gathered from such a dissection as that represented in fig. 1, Pl. LXXXI., that the main axis of the cephalopodium, as indicated by the general trend of the tentacular sheaths, does not coincide with the skeletal axis but describes an angle with it. I shall refer to this matter again under the heading "Flexure and Orientation," but meanwhile I cannot help thinking that the occurrence of conflicting axes in relation to the cephalopodium of *Nautilus* may have morphological significance, as affording evidence of profound topographical changes which have upset the primitive axial simplicity. Such an axial disturbance is no longer apparent in the Dibranchiata, so that whatever it may indicate, it is at all events a remarkable feature in the organisation of *Nautilus* and should be, though it never has been, taken into account.

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[1] "Kopfknorpel" of Keferstein 1865 and Haller 1895.

[2] "Within the crura of the funnel" (Owen).

[3] The endochondral sinus was described by Owen in the following words (memoir, p. 16):—"In the body of the skeleton is excavated a large sinus, which receives the contents of the veins of the head and funnel, and empties itself into the commencement of the great dorsal vein." The "great dorsal vein" of course refers to the *vena cava* which is quite superficial and ventral, as Owen correctly states on p. 27 of his memoir.

[4] Art. "Mollusca," *Encyc. Brit.* 9th edit. 1883, *Zool. Articles* (1891), p. 143.

The limit of the extension of the anterior cornua into the crura of the funnel is superficially indicated on each side by the presence of a limbate border (*l*). These cornua do not reach to the base of the tongue-like valve which is inserted upon the inner surface of the dorsal wall of the funnel.

The posterior cornua underlie the optic ganglia, the olfactory labyrinths (rhinophores) and the otocysts in the order named (cf. Pl. LXXXI. fig. 5), but do not embrace these structures. Into the hinder extremities of the posterior cornua are inserted the retractor muscles of the buccal cone (Pl. LXXXI. fig. 7), and the angles in which the insertion takes place constitute deep pits in the fundus of the peristomial haemocoel.

The funnel itself comprises several regions which differ in colour, texture and function. Its anterior and posterior portions are separated from one another by the anterior cornua and body of the cartilage. At the forward limit of the latter there occurs externally a peculiar border or *limbus*, the *limbus infundibuli* (*l*). If the funnel be cut across behind the *limbus* the whitish *crura infundibuli* penetrated by a pair of subcylindrical muscles, the *levatores infundibuli* of Owen, lying in their own venous sinus on each side, are seen to be clearly separated by the anterior cornua of the cartilage, from the soft brownish yellow *alae infundibuli* which extend backwards and dorsally to the base of the nuchal membrane. (Pl. LXXXII. fig. 3.) It is one of the best known peculiarities of the organisation of *Nautilus* that the funnel is cleft down the ventral surface, so that its flaps overlap and present a free border throughout their entire length. The anterior portion of the free borders of the flaps belongs to the region of the *crura*, and the posterior portion to that of the *alae*, although of course quite continuous. The *crura* are united together dorsally by the thin median wall of the funnel which rests in the infundibular fossa of the great oral sheath and carries, on its inner surface, the large valve of the funnel. Behind this thin-walled anterior portion, the dorsal wall of the funnel, between the *alae*, is greatly thickened owing to the presence of the spongy *compressor* muscle, the transverse fibres of which are inserted into the median keel of the cartilage (*carina cartilaginis*).

In the fresh condition the integument which covers the compressor muscles and the adjoining surface of the *alae infundibuli* is found to be a slimy, mucous membrane, forming two large pads meeting in the middle line and constituting the *mucus-gland* of the funnel. It is interesting to note that Jatta[1] has interpreted the funnel-organ of Dibranchiate

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[1] Jatta, G., "Sopra l'organo dell' imbuto nei Cefalopodi." *Boll. Soc. Napoli* (Ser. 1) vii. 1893, pp. 45—60, Tav. iv. The funnel-organ is sometimes called the "Organ of Verrill" or "Organ of Müller." Cf. Hoyle, W. E., "Observations on the anatomy of a rare Cephalopod (*Gonatus fabricii*)." *P. Zool. Soc. London*, 1889, p. 128.

Cephalopoda as a mucus-gland, and has further homologised it with the pedal gland of the Gastropoda.

After comparing the figures published by Jatta, relating to the funnel-organ of *Sepia officinalis, Octopus vulgaris* and other species, I have no doubt that the funnel-gland of *Nautilus* is an organ homologous with the corresponding structure in the funnel of other Cephalopoda. I have not made sections through this gland, and shall have no further opportunity of doing so, but I have really no hesitation in the matter notwithstanding this omission (cf. Pl. LXXVI. fig. 1).

The funnel-organ of *Nautilus* passes laterally into the *alae infundibuli*, and posteriorly it is attached to the ventral surface of the skin covering the shell-muscles by an elongated *limbus*. I observed a network of what I took to be venous channels below the *mucosa* of the funnel-organ, and two large veins passing from the *limbus* into the *vena cava*. (See figures on Pl. LXXXII. and LXXXIII.)

The cartilage forms a very incomplete wall to the endochondral sinus, only the ventral and lateral sides being bounded by massive cartilage, while dorsally there is a narrow bar of cartilage (*arcus cartilaginis*) which forms two bosses projecting into the peristomial haemocoel between the pedal and visceral commissures. Between the *arcus* and the pedal commissure are to be seen two orifices which represent main conduits leading from the peristomial haemocoel to the endochondral sinus (Pl. LXXXII.). Behind the *arcus* occurs the insertion of the inferior retractor muscles of the buccal cone into the body of the cartilage on each side.

The infundibular nerves arise from the pedal commissure and run straight forwards into the *crura infundibuli* dorsad and ectad of the tubular sinuses, in which the abovementioned levator muscles lie. Their topography will be elucidated in the chapter on the peristomial haemocoel.

In concluding the present chapter, I should like to emphasize the view that the capito-pedal cartilage of *Nautilus* is to a large extent a funnel-cartilage, and is probably not directly homologous with the cephalic cartilage of Dibranchs, but related to the latter through substitution. It is of course obvious that the principle of substitution is apt to become little more than a form of words, and to convey no true image to the mind. In regard to the endoskeleton of Cephalopoda the idea which is present to my mind is the following. The cephalic cartilage is to the Dibranchs what the capito-pedal cartilage is to *Nautilus*, but the former is not to be identified with the latter, and does not merely represent a specialisation of it. If this be so we might expect to find traces of a true capito-pedal or funnel-cartilage in the Dibranchs, and indeed a pair of siphonal cartilages[1] curiously recalling the cornua of the cartilage of *Nautilus*, has been discovered by Hoyle[2] in the remarkable and, in more than one sense, primitive genus *Gonatus*. Without venturing to express the definite opinion that these apparently rudimentary siphonal cartilages of *Gonatus* may represent vestiges of a capito-pedal cartilage such as occurs in the still more primitive genus *Nautilus*, I think the suggestion may be one worthy of the attention of teuthologists, although the fact that they occur in the ventral wall of the siphon of *Gonatus* might be thought to militate against this view. Still the anterior cornua of the cartilage of *Nautilus* penetrate into the ventral wall of the funnel.

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[1] The funnel of Cephalopoda is often quite properly called the *siphon* but the latter term is also quite improperly applied to the siphuncle of Tetrabranchiates, and for this reason I have avoided its use.

[2] Hoyle, W. E., "Observations on............*Gonatus fabricii*," *op. cit.*, see p. 120. Cf. also on *Gonatus*, the same author's Report on the Cephalopoda collected by H.M.S. Challenger, 1886, p. 173.

9. Digital and Ophthalmic Tentacles.

The head or cephalopodium of *Nautilus* comprises the better half of the animal, and represents a complication of organs and appendages performing divers functions. The body-wall in this region is composed in the main of a thick coriaceous integument, which presents a dorsal convexity formed by the mottled brown-coloured hood, and three deep concavities, anterior, posterior and ventral. The anterior deepest concavity is the *fossa buccalis,* which is surrounded by the tentacular crown and lodges the great buccal cone; the posterior concavity is the *fossa nuchalis* which receives the *anfractus* of the shell, and gives origin to a muscular flap, the semilunar nuchal membrane; finally the ventral concavity is the *fossa infundibularis,* which varies somewhat in depth according to the state of muscular contraction of the parts concerned in its formation, and is exactly suited to receive the funnel.

The cephalopodium of *Nautilus* consists of a tentacular crown disposed about the mouth in the form of an oral sheath, and composed of two whorls, outer and inner. The outer circlet[1] of tentacles comprises the "digital processes" of Owen, while the inner circlet consists of the so-called "labial processes," but the latter is an unfortunate term, since the actual buccal orifice is provided with a prominent lip surrounding the mandibles and richly furnished with labial papillae. I therefore propose to refer to the tentacles generally, whether belonging to the outer or to the inner whorl, as digital tentacles. The two tentacles, the one in front of, and the other behind the eye on each side, which Owen named "ophthalmic tentacles," really belong to the outer whorl, but have become so modified in function and position as to require separate treatment.

The tentacles arise from the bottom of profound sheaths, within which those of the outer whorl are completely retractile and those of the inner whorl partially so, but in either case it is at once apparent that the tentacles are essentially *marginal appendages.*

The digital tentacles have been more particularly described as to their structure and distribution by Owen (1832), Valenciennes (1841), Owen[2] (1843), Lankester and Bourne (1883), Vayssière (1896), Willey[3] (1897), Griffin[4] (1898). These tentacles have in general a trihedral form tapering slightly towards the tip, and are divided by shallow annular grooves into a large number[5] of articulations, the grooves being deeper on the inner sides which form the bases of the trihedra, so that a series of transverse ridges is produced, by means of which the tentacles are able to adhere to surfaces in a manner analogous to the action of the feet of a gecko. When attached to a rough surface by means of the suctorial ridges the tentacles may be drawn out to a great length in all directions, and hold on to their support with so much tenacity that sometimes when I forcibly detached the animal some of the tentacles broke off and remained fixed to the substratum. The suctorial ridges of the tentacles have a pale neutral tint in the fresh state, while the crests and sides of the trihedra are distinguished by a deep brown pigment. The tentacles which thus act in a way resembling the arms of the Dibranchiate Cephalopoda are the digital tentacles of the outer whorl. They have an adhesive, prehensile and tactile function.

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[1] The outer whorl is the same as Lankester's "annular lobe" (Article "Mollusca," *Encyc. Brit.* 9th Edit.).

[2] Owen, R., "On the structure and homology of the cephalic tentacles in the Pearly *Nautilus*." *Ann. Nat. Hist.* XII. 1843, pp. 305—311, 2 figg.

[3] Willey, A., "The pre-ocular and post-ocular tentacles and osphradia of *Nautilus*." *Quart. J. Micr. Sc.* Vol. 40, April 1897, p. 197; also in same volume (Aug. 1897), "The adhesive tentacles of *Nautilus*...............," p. 207.

[4] Griffin, L. E., "Notes on the tentacles of *Nautilus pompilius*." *Johns Hopkins Univ. Circ.* XVIII. Nov. 1898, p. 11; reprinted in *Ann. Nat. Hist.* (7) III. Feb. 1899, p. 170.

[5] Sixty to one hundred, according to Mr Griffin.

In the middle of each tentacle runs a large axial nerve, which originates directly from the ganglionic nerve-centre and presents, as was first noted by Griffin, a series of slight ganglionic enlargements at its periphery, in correspondence with the annulation of the tentacle. In sagittal section the axial nerve is seen with its peripheral ganglion cells which constitute an almost unbroken layer on the ventral side of the nerve, that is on the side nearest to the suctorial ridges, but on the opposite side are segregated into groups. The suctorial ridges appear as bold outstanding nearly flat-topped excrescences slightly convex, with a tendency to imbricate at their edges. They are covered with a high and very dense epidermis which passes abruptly into the indifferent layer which lines the intervening grooves. Below the nerve the tentacle is traversed by an artery, and below that again, a venous channel[1]. Owen (1843) graphically described the dense central tissue which protects the nerve and artery, from whence radiating fasciculi proceed to the periphery with longitudinal muscular bundles in the meshes. He also pointed out how similar requirements elsewhere are met by analogous structure. Thus "the mechanical arrangement of the contractile fibres is very similar to that of the complex muscles described by Cuvier in the proboscis of the elephant. The attenuation and elongation of this brobdignagian [*sic*] tentacle must be effected without compressing the central breathing-tubes and the transverse fibres accordingly radiate from the dense ligamentous tissue which surrounds the tubes." We may add that a closely analogous structure is met with in the proboscis of the Enteropneusta. The arms of the other Cephalopoda are also built upon the same plan. Owen duly noted the suctorial ridges which he described as presenting "the appearance of a number of close-set transverse plates." He says further that "this modification must increase the prehensile and sentient properties of the inner surface of the tentacle, and it is on the corresponding part of the larger and fewer tentacles of the Dibranchiate Cephalopods that the acetabula are developed." Again on p. 310 (1843) he states that "the prehensile surface of the tentacula of the *Nautilus* is made adhesive, after the type of the simple laminated sucker of the *Remora*." Finally the primary import of the tentacles of *Nautilus* is "plainly indicated by the direct derivation of their central nerve from the cephalic ganglion."

These quotations serve to show that Owen had acquired a very just appreciation of the general nature of the digital tentacles, although it should be noted that the fact of adhesion by means of what I have called the suctorial ridges had not then been established.

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[1] A good representation of a transverse section through a tentacle is given by Vayssière in *Ann. Sci. Nat.* (8) II. 1896, Pl. 19, fig. 19.

Owen's paper of 1843 was written by way of reply to Valenciennes (1841), who had compared the sheathed tentacles of *Nautilus* not with the arms of the Dibranchs, but with the suckers which are borne upon the arms, the sheath corresponding with the cupule of the sucker and the tentacle with the caruncle. This interpretation was supported by Professor Lankester (1883, *Encyc. Brit.*), and is in fact widely held[1]. For my part I am unable to subscribe to the very ingenious theory of Valenciennes for reasons which I shall submit later. Valenciennes not only compared the sheathed tentacles of *Nautilus* with the acetabula of Dibranchs, but grouped them together in such a way as to show a correspondence with the eight arms of an Octopod. His point of view was undoubtedly ingenious though artificial. In his Pl. XI. fig. 2, he represents an ideal section across the cephalopodium, in which the tentacles are associated together into four paired groups represented, as he claims, in actual anatomy by eight muscular peduncles. These groups are as follows:—

1. Hood and accessory sheath.
2. Mass of the external digital lobe.
3. Internal labial lobe.
4. Inferior labial lobe of ♀.

Valenciennes explained his position in these words (pp. 275—276):—"Dans cette manière de voir je ramène au nombre ordinaire des bras des céphalopodes en général le nombre de ceux de nautile, puisque les quatre-vingt-huit cirrhes, considérés avant moi comme bras du nautile, ne sont plus que des appendices sortant des ventouses allongées en gaînes.............Mais ne voulant pas pousser ces analogies au-delà de ce qui peut en quelque sorte se démontrer, je me hâte d'ajouter que si les bras du nautile ressemblent à ceux du poulpe par leur position autour du bec, ils sont toutefois bien différents par leur forme et leur structure, malgré l'espèce d'analogie que nous venons d'indiquer entre les cirrhes de l'un et les ventouses de l'autre."

Not the least noteworthy feature in regard to the digital tentacles of *Nautilus*, especially those of the outer whorl, is their striking constancy in number and position. This is the more remarkable because their number is large and their position apparently arbitrary. Owing to the latter circumstance it has not been easy to arrive at a satisfactory method of enumeration of the tentacles, which is a matter of statistical interest and incidentally of morphological importance.

The sheaths of the tentacles cohere in such a manner that they form a fleshy mass in which the tentacles themselves appear to be arranged without regard to any law or order, but a critical examination discloses, to my thinking, a possible means of interpretation which the diagrams on Plate LXXXI. will serve to elucidate.

The method of enumeration which I have to suggest was acquired independently after many attempts to arrive at a settlement. Subsequently I became acquainted with

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[1] *E.g.* it is the view expressed in Professor Arnold Lang's *Lehrbuch der vergleichenden Anatomie*, 1st edit. 1892, p. 691.

Professor Vayssière's efforts in this direction[1]. As it is, in my opinion, a subject of considerable relative importance, I will venture to quote the passage from M. Vayssière's memoir bearing upon this point:—" S'il est facile de numéroter les bras d'un Céphalopode Dibranchial vu leur nombre restreint, il n'en est pas de même pour ceux du Nautile; il est incontestable que je désignerai sous le numéro 1 celui qui forme la moitié du capuchon céphalique, c'est lui qui est le plus dorsal. Le numéro 2 pourra s'appliquer au premier tentacule qui longe le bord du capuchon en contractant adhérence avec lui sur presque toute sa longueur; mais pour les autres quel ordre faudra-t-il suivre pour les numéroter? est-ce un peu au hasard, en allant de dedans en dehors et en s'avançant progressivement vers l'entonnoir, ou bien faut-il tenir compte de certains groupements de trois à quatre tentacules qui forment des sortes de verticilles se recouvrant? Ce dernier mode serait préférable si l'on ne constatait pas quelques variations dans la disposition de ces groupes; aussi vaut-il mieux s'en tenir à la numérotation de la face dorsale vers la face ventrale, en allant toujours par rangées transversales de l'intérieur vers l'extérieur."

The desirability of a definite method of enumeration by which the individual members of a relatively constant series can be recognised, will be obvious to all who interest themselves in meristic phenomena, and especially to those who may have opportunities for studying *Nautilus*.

The following tabulations display the differences in the application of my method as compared with that of Professor Vayssière, and I hope to show by what has preceded as well as by what shall follow, that this is a point about which it is worth while to differ.

Table A. Enumeration of the tentacles of the outer circlet in *Nautilus* according to my standard.

Willey	Vayssière[2]	Willey	Vayssière[2]
1	1	11	9
2	2	12	6
3	3	13	4
4	5	14	8
5	7	15	11
6	10	16	13
7	14	17	18
8	19	18	15
9	16	19	17
10	12		

Table B. Enumeration of the outer tentacles according to Vayssière's standard.

Vayssière	Willey	Vayssière	Willey
1	1	11	15
2	2	12	10
3	3	13	16
4	13	14	7
5	4	15	18
6	12	16	9
7	5	17	19
8	14	18	17
9	11	19	8
10	6		

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[1] Vayssière, A., " Étude sur l'organisation du Nautile." *Ann. Sci. Nat.* (8) II. 1896, see p. 162 and Pl. 17, fig. 8.

[2] Vayssière, *op. cit.* Pl. 17, fig. 8. The figure relates to a male *N. macromphalus*.

The above tables seem to betray ineradicable divergencies, due merely to different points of view. There is, however, one door left open for immediate criticism. It might at least have been expected that there would be agreement as to the first and the last, but such is not the case. Vayssière's nineteenth tentacle is my eighth, and my last is Vayssière's seventeenth.

It was admitted by Owen and his successors that the main bulk of the hood consists of "two digitations conjoined along the mesial line[1]." "The median antero-posterior line traversing this hood exactly corresponds to the line of concrescence of the two halves of the fore-foot, which primitively grew forward, one on each side of the head, and finally fused together along this line[2]." Seeing that the lateral portions of the hood are actually formed by the cohesion of the sheaths of the second pair of tentacles with the main body of the hood, it appears reasonable to infer that the latter arose by concrescence of the sheaths of the first pair. The median portion of the hood of *Nautilus* is thus taken to represent a *dorsal symphysial tract*.

I have found no reference to the occurrence of a *ventral symphysial tract*[3] and yet, I think, that is the nature of the bridge which forms the fundus of the concavity which lodges the funnel, and at the same time completes the outer circlet (annular lobe of Lankester) across the ventral median line. At the corners of this tract are placed the tentacles of the nineteenth pair, in very much the same way as the tentacles of the first pair occur near the outer borders of the median portion of the hood, and I think it likely that this ventral tract owes its origin to the concrescence of the sheaths of the last pair of tentacles, just as the dorsal tract admittedly represents the fused sheaths of the first pair. An indication of the bilateral constitution of the ventral tract is furnished by the mesial line which divides the laminae of the mucous gland which develops upon its inner surface in the female[4]. If it is true that there is a ventral symphysial tract, then it is clear that the tentacles which are most intimately associated with it and immediately border it are to be reckoned as the last of the series.

Assuming then that my identification of the nineteenth pair of tentacles of the outer circlet is correct, it still remains to justify the enumeration of the tentacles which intervene between the first and the last. Taking into consideration their evident character as marginal appendages of an annular lobe, we may further assume that the border out of which they arose was not plain but frilled like an undulating membrane, and that the sinuations underwent concrescence, thus producing a thick matrix in the midst of which the tentacles occur, in places, three or even four deep. By slicing off the upper portion of the sheaths of the outer tentacles, it may be at once seen that the sequence of the numbers one to eight and nine to thirteen, in my enumeration, is exactly such as would result from the concrescence of a frilled border, and closer examination will show that the remaining numbers follow suit in the order given.

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[1] Owen, Memoir 1832, p. 13. Owen seems to have erred somewhat in his counting of the tentacles through anxiety on behalf of even numbers. The passage runs as follows:—"Of the digital processes nineteen have been enumerated on either side; but as the hood has two perforations anteriorly from which tentacles similar to those of the digitations are also protruded, we may consider this part as two digitations conjoined along the mesial line, and so reckon with Rumphius the even number of twenty digitations on either side of the head."

[2] Lankester, E. R., Article "Mollusca," *Encycl. Brit.*, 9th edit., republished in *Zoological Articles*, 1891, see p. 137.

[3] Except perhaps in the memoir by Valenciennes (1841), who describes the two inferior arms as being united below by a thin plate hollowed out to receive the funnel, while on the inner surface of the plate, on each side of the median line of junction, there is in the female a lamellated organ, the same which has recently been shown by Mr Graham Kerr to serve as a receptacle for the spermatophore.

[4] Cf. Kerr, J. G., "On some points in the Anatomy of *Nautilus pompilius*." *Proc. Zool. Soc. Lond.* 1895, see Pl. 39, fig. 3. I shall subsequently refer to this laminated gland as the "Organ of Valenciennes."

Not only are number and plan of distribution of the outer tentacles identical in male and female, but they are also the same in the three species, *N. pompilius*, *N. macromphalus*, and *N. umbilicatus.* In all cases the outermost of the series are numbers 5, 6, 7, and 8, of which the first three appear to be grafted upon the external surface of the circlet, and are much shorter than the rest of the tentacles whose sheaths form the outer wall of the crown, number 6 especially lagging far behind the others, its sheath being produced into a prominent lobe behind. The prism-shaped sheath of the 7th tentacle is always accurately wedged into a deep groove between the 9th and 10th; that of the 6th fits into a similar groove between the 5th and 11th, while the 5th itself is ensconced at a higher level between the 4th, the 12th and the 11th. There is a shallow concavity between the sheaths of the 9th and 17th tentacles which receives that of the 8th; the inner border of this concavity is furnished by the sheath of the 17th, and so shuts off the 9th from participation in the lateral wall of the great ventral concavity of the annular lobe which I have called the *fossa infundibularis*; this wall is actually formed by the coalescent sheaths of the 8th, 17th and 19th tentacles.

If we now look for some corroboration of the sequence of tentacles which I have suggested above, from a consideration of the nerves which are distributed among them, we shall find to a certain extent a welcome confirmation. My series 5—8 inclusive, represented in Professor Vayssière's scheme by the numbers 7, 10, 14 and 19, are found to receive their nerves in absolute sequence (Pl. LXXXI. fig. 6, and Pl. LXXXII. fig. 6). The most direct manner of procedure for exposing these nerves, and I believe the technically correct method, is to remove one of the *alae infundibuli,* and then by horizontal incisions through the cartilage and coriaceous tissue at the base of the cephalopodium gradually to expose the sense-centres of one side. In this way it is impossible to overlook the otocyst which escaped both Owen and Valenciennes, being first found by Macdonald (1855, *Phil. Trans.*). In front of and partially concealed by the otic capsule appears the dark mass of the pedal ganglion. Upon exposing this portion of the "syncerebrum[1]" without too much displacement of neighbouring organs, three nerve-roots almost simultaneously appear to the view of the dissector, and upon tracing these to their destination I was somewhat agreeably surprised to find that they were the nerves belonging to the sixth, seventh and eighth digital tentacles according to my system of enumeration (Pl. LXXXI. fig. 6). Continuing the dissection by turning aside the olfactory labyrinth (rhinophore), we find that contiguous and level with the root of VI is that of V (Pl. LXXXII. fig. 6). The large nerve lying at a slightly deeper level next to V in the dorsad direction is IV, at the base of which the root of III arises apparently as a branch, but the appearance of branching is attributable to the fact that the two nerves are for a very short distance enclosed in a common perineurium. The next nerve dorsad of III and IV is II, which has a length of about 21 mm. from its origin to its insertion into the base of the second tentacle. Then comes I with a length of 28 mm. giving off collateral branches to the substance of the hood. By cutting through and turning back the roots V, VI, VII and VIII, those of IX, X, XI and XII are exposed in sequence at a deeper level, IX occurring between VIII and VII, X between VII and VI, XI in front of VI; XII lies at a slightly deeper level, and bears the same relation to XI that IV does to V. The sequence of IX, X and XI is as striking as that of V, VI, VII and VIII but I am inclined to lay special stress upon the latter sequence. The root of XVII lies opposite to VIII but at a deeper level than the series IX, X and XI.

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[1] The term applied by Professor Lankester to a compound cephalic ganglionic mass in contrast with "archicerebrum" where the cephalic centre comprises the cerebral ganglia only.

Without attempting the impossible task of proving to complete satisfaction the truth of the entire sequence suggested by me, I think it is legitimate to select a small group as a test case, and in this sense I may repeat the fact, which is not at all obvious without actual demonstration, that the nerves V, VI, VII and VIII occur in indubitable topographic sequence (Pl. LXXXII. fig. 6).

Before devoting a few lines to a consideration of the inner whorl of the cephalopodium, it is necessary to turn our attention to the *ophthalmic tentacles* which occur in front of and behind the eye. These resemble the digital tentacles in shape and annulation, but differ, in that the sulci are much deeper on the side corresponding to that on which the suctorial ridges of the former are placed, so that the tentacles are converted into distinctly lamellate appendages, and when examined in the fresh state under the microscope, the grooves and lamellae are found to be covered with vibratile cilia (Pl. LXXIX. fig. 14). The suctorial ridges of the outermost digital tentacles may in favourable specimens be seen to become more and more prominent and lamelliform towards the free ends, and I have observed that when the main portion of the tentacles has been affixed to a surface, the tips of the tentacles which probably exercise some kind of tactile function were free. I have never seen cilia at any part of the true digital tentacles.

The ciliated lamellae of both the pre-ocular and the post-ocular tentacles are directed forwards, and the shafts of the tentacles when extruded are kept in an attitude of attention, the anterior being directed obliquely outwards and forwards, the posterior obliquely outwards and backwards, but nearly or quite straight (cf. Pl. LXXVII. figg. 3, 6).

I came to the conclusion[1] that the ophthalmic tentacles of *Nautilus* while homologous with the adhesive digital tentacles have become modified to serve as accessory olfactory organs, and that the ciliated ridges represent olfactory lamellae. In the living state the ophthalmic tentacles afford a strong contrast to the brown digital tentacles by reason of their nearly uniform white colour; there is a small trace of brown pigment in the annulations and at the edges of the lamellae, but when viewed under water the general colour is white. They are also characterised by increased sensibility. Whereas the digital tentacles can be touched without being retracted in consequence, the slightest contact with a foreign body occasions the instant withdrawal of the ophthalmic tentacles into their sheaths.

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[1] Willey, A., "The pre-ocular and post-ocular tentacles............of *Nautilus*." *Quart. J. Micr. Sc.* Vol. 40, 1897, p. 199.

In my paper on this subject (1897) I added the following remarks:—"The presence of accessory olfactory tentacles in *Nautilus* can, I think, be related to an essential bionomical difference between the existing Tetrabranchiata and the Dibranchiata. *Nautilus* finds its food chiefly by the sense of smell, while............the Dibranchiata with their remarkably perfect eyes pursue their quarry by the sense of sight. This difference......... is further emphasised by the different modes adopted by the natives for trapping these animals.

"One of the surest ways of obtaining *Nautilus*, and in fact the method by which I have obtained most of my specimens at Lifu, is to bait the fish-basket with the cooked and bruised exoskeleton of *Palinurus*.........wrapped up in cocoa-nut fibre like a small parcel and placed in the fish-trap overnight. There is nothing to be seen but ....something to be smelt, and by this means I have obtained as many as ten *Nautilus* at one time. For taking *Octopus* the natives of Lifu employ a very different method. A rounded oval piece of stone backed by a well-fitting piece of the shell of a species of *Cypraea*, to which are added pieces of leaf to simulate legs and tail, is dangled along the surface of the water at the end of a line. The natives say that the *Octopus* mistakes this for a rat, against which it has a special grudge; but......... the fact remains that *Octopus* attacks this singular non-scented contrivance and so is captured." The Lifuan name for this simple apparatus is "athy."

One of the most interesting points about the ophthalmic tentacles concerns their innervation, regarding which there has been serious disagreement among zoologists, but I hope to show in this matter that the facts of the case are beyond the reach of controversy. Owen's figure (1832) of the central and peripheral nervous system of *Nautilus* conveys an excellent general idea of its main characters, but is too diagrammatic in its representation of details to be of much assistance at this particular juncture. Valenciennes (1841, p. 288, Pl. VIII. fig. 2) described the nerves of the ophthalmic tentacles as arising from the cephalic ganglionic ring, separated from each other on each side by a wide interval which is occupied by the optic and true olfactory nerves, so that according to him the nerve which supplies the posterior ophthalmic tentacle arises dorsad and mediad of the optic nerve. Valenciennes appears to have overlooked the buccal or stomatogastric nerves, of which there are two pairs arising from the cerebral (supra-oesophageal) commissure, and hence probably misinterpreted one of the latter as the nerve to the posterior ophthalmic tentacle (cf. Pl. LXXXIII. figg. 28 and 29). Nevertheless von Jhering[1], who was the first to note the existence of a stomatogastric or "sympathetic" nervous system in *Nautilus*, confirmed Valenciennes' account of the nerves to the ophthalmic tentacles, which we may be allowed to call the ophthalmic nerves in place of a better name although it is of course open to misinterpretation; but I am not prepared to suggest a new name. Von Jhering says that the posterior ophthalmic nerve is the last nerve which leaves the supra-oesophageal ganglion dorsad of the optic nerve. As a matter of fact this last cerebral nerve is the second buccal or stomatogastric nerve which von Jhering overlooked. With regard to the anterior ophthalmic nerve, von Jhering also confirmed Valenciennes in these words:—"Nach innen und unten vom Sehnerven entspringen vom oberen Theil des vorderen Suboesophagealstranges der Geruchsnerv.........und der Nerv des vorderen, unteren oder ventralen Augentakel." This of course is a very broad statement, and in fact the true olfactory nerve does lie below the optic ganglion, but it does not arise from the anterior (pedal) commissure (cf. my Pl. LXXXI. fig. 6).

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[1] Jhering, H. v., "Vergleichende Anatomie des Nervensystemes und Phylogenie der Mollusken," Leipzig, 1877, pp. 262 and 264. Von Jhering's account of the stomatogastric system has been essentially corrected and amplified by Mr J. Graham Kerr (*op. cit.* 1895), whose description of these nerves I can confirm.

Pelseneer[1] regarded the ophthalmic tentacles of *Nautilus* as belonging essentially to the head, and as homologues of the labial and nuchal cephalic tentacles of Gastropoda, and therefore not homodynamous with the digital tentacles of *Nautilus*. While advocating the theory of the pedal nature of Cephalopod arms in general, he insists on the cephalic nature of the ophthalmic tentacles of *Nautilus*, saying in a foot-note: "Il est inexact de dire, comme von Jhering, que le tentacule ophthalmique antérieur est innervé par le ganglion infra-œsophagien antérieur. Tout comme le nerf olfactif, le nerf du tentacule ophthalmique antérieur sort de la partie latérale extrême du ganglion supra-œsophagien, ainsi que le montrent les figures précitées de Valenciennes."

It is therefore quite clear that the ophthalmic tentacles of *Nautilus* occupy a crucial position as between head and foot, and it is the more desirable to ascertain the exact origin of their nerves. The most recent author who has dealt with this matter is Dr L. E. Griffin[2], who describes an accessory nerve-trunk associated with the axial nerve-trunk traversing the body of the tentacle, and adds that "the nerves of the two ocular tentacles of each side are branches of a nerve which comes off from the pedal ganglion near the outer end, which also sends branches to the hood."

According to my own observations Dr Griffin's statement comes nearer to the truth than any other relating to this point with which I am acquainted, but I do not agree with him that the ophthalmic nerves are branches of the hood-nerve.

The ophthalmic nerves in fact arise by independent roots from the dorsal border of the pedal ganglion[3]. The anterior ophthalmic nerve arises close behind the capitular (hood) nerve, but is surrounded by its own perineurium, and proceeds upwards and slightly forwards to the base of the tentacles (Pl. LXXXII. fig. 6). The posterior ophthalmic nerve again arises independently, close behind its colleague and holds a pronounced recurrent course, passing backwards to its tentacle in the wall of a sinus in which the optic ganglion lies. The posterior ophthalmic nerve does therefore not arise dorsad of the optic nerve, but it passes backwards from its origin in the pedal ganglion (Pl. LXXXII. fig. 6). The position of the ophthalmic nerves in relation to the digital nerves shows that the ophthalmic tentacles are in sequence with the digital tentacles, and that the posterior ophthalmic tentacle is the first, the anterior ophthalmic tentacle the second, and the capitular (first digital) tentacle the third member of a continuous morphological series, the remaining digital tentacles following in their due order.

In the diagrams of transverse sections on Pl. LXXXI. the ophthalmic tentacles are omitted, and I have also not reckoned them numerically with the digital tentacles, but their morphological valency as the first two tentacles of the outer whorl of the cephalopodium of *Nautilus* is I think clear, and I shall again refer to the recurrent nerve of the posterior ophthalmic tentacle[1].

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[1] Pelseneer, P., "Sur la valeur morphologique des bras et la composition du système nerveux central des Céphalopodes." *Arch. Biol.* Vol. VIII. 1888, see p. 730.

[2] Griffin, L. E., "Notes on the tentacles of *Nautilus pompilius*." *Johns Hopkins Univ. Circ.* Vol. XVIII. Nov. 1898.

[3] For the present I use the term "pedal" in this connection as being less unwieldy and less inaccurate than "infra-oesophageal." It might be called by an indifferent name, such as "coronal ganglion." "Brachial ganglion" implies too much. "Tentacular ganglion" would also mislead.

The *inner whorl* of the cephalopodium is incomplete dorsally, and moreover it is broken up into distinct tentaculiferous and lamelligerous lobes which have become more or less specialised as accessory sexual organs, and exhibit profound sexual differences which are tolerably familiar to malacologists. There are two principal groups of tentacles of the inner whorl which may be described as *extrabuccal* and *infrabuccal*, and correspond to Owen's "external labials" and "internal labials" respectively. The objections to Owen's terminology are firstly that the epithets "external" and "internal" obscure the view that the tentacles belong to an inner whorl, and secondly the expression "labial" is inappropriate and apt to cause confusion with the labial papillose fringe which surrounds the jaws.

In the female the extrabuccal lobes carry twelve ordinary tentacles on each side, of which eight are disposed in a descending and four in an ascending series. The lobes themselves consist of the coalescent sheaths of the tentacles borne upon a fleshy basis which rises up from the fundus of the *fossa buccalis*. The extrabuccal lobes adhere ventrally to the inner surface of the outer whorl[2] by means of an *intercoronal membrane* which proceeds on each side from the ventral border of the lobe (cf. Pl. LXXX. figs. 7 and 8, *i*).

In the male the extrabuccal tentacles are subdivided into three groups, an upper series of eight tentacles with coalescent sheaths, a middle set of three, and a single ventral free tentacle. The free tentacle is usually found to nestle within a groove formed by a vertical flap which grows out from the sheath of the first tentacle of the middle set or the ninth of the entire series, or it may follow simply at the end of the series. The middle set comprising the ninth to the eleventh extrabuccal tentacles, together with the free twelfth tentacle, constitute a natural group of four which are known as the *spadix* on the one side and the *antispadix* on the other. The *intercoronal membrane* arises in the male from the lower border of the upper set of coalescent tentacular sheaths (1—8), and passes unattached in front of the tetrad group to its insertion into the inner wall of the outer (annular) lobe.

The ventral or infrabuccal lobe of the inner whorl is modified in both sexes to form a special *infrabuccal apparatus*. In the female it consists of a median laminated organ flanked on each side by a uniserial row of 12—14 tentacles; the lamellae are modified tentacles and retain their apices (Pl. LXXIX. fig. 6, and Pl. LXXX. fig. 11). In the male there are no unmodified tentacles remaining in connection with the infrabuccal apparatus, which is completely metamorphosed into a laminated organ, known as Van der Hoeven's organ, retractile within a pouch and closely adherent to the ventral integument of the buccal cone.

I do not propose to enter upon a long description of these structures, partly because this has already been done by others, and partly because I was unable to ascertain the manner in which the various parts are brought into action.

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[1] In my experience the most suitable material for the successful dissection of the tentacular nerves of *Nautilus* consists of soft specimens and not of such as have become too hard under preservation.

[2] The outer whorl is the "oral sheath" of Owen, the "annular lobe" of Lankester.

The spadix is a composite erectile organ (Pl. LXXVIII. fig. 4) which occurs indifferently on the right or left side of the cephalopodium. It was originally described by Van der Hoeven[1], and has since been treated in greater detail by Professors Haswell[2] and Vayssière[3]. This organ shows a gradual development from the early to the adult life of the animal, only attaining its full growth at sexual maturity (cf. Pl. LXXX. figg. 3—7 and Pl. LXXIX. figg. 9 and 10). The ninth extrabuccal tentacle constitutes the *glans* and its sheath, the *prepuce.* The latter gives rise to a free fold along its outer border, and at the summit bears a large thick glandular cushion covered with bordered pits, which may be described as the *preputial gland.* The tenth tentacle (the second of the spadix) is a fleshy flattened appendage strongly ribbed upon its glandular surface. The third tentacle of the spadix (eleventh of the series) is also a flattened foliaceous appendage, but in place of the transverse costae of the preceding tentacle, it presents a marvellous system of glandular crypts, producing the appearance, as Professor Haswell pointed out, of a minute honeycomb. The last tentacle, the twelfth extrabuccal, is somewhat enlarged, but otherwise undergoes comparatively little modification and is partially concealed, on the outer aspect of the spadix, beneath the flap of the prepuce. The second tentacle of the spadix may be distinguished as the *costate tentacle,* the third as the *tessellate tentacle,* and the fourth as the *free tentacle* or cirrus.

Like all the other accessory sexual organs of both male and female, the spadix manifests a gradual development *pari passu* with the growth of the animal. I use the word "development" in contrast with "growth" to express the fact that in the young *Nautilus* the character of the spadix is quite different from the adult structure of the organ.

The smallest *Nautilus* which I ever obtained was a male *N. pompilius*[4] with the following dimensions:—

Length from root of siphuncle to mid-anterior point of hood (measured along the dorsum)[5]	25 mm.
Length of hood along middle line	10·5 „
Breadth of body across middle of eyes	15 „

The shell was perforated at the umbilicus and contained thirteen air-chambers.

At this stage it is not possible to say upon which side of the cephalopodium the definitive spadix will appear, the two groups of four tentacles—numbers 9 to 12 of the inner whorl—being almost exactly alike, notably in regard to the tardy development of the 10th tentacle (Pl. LXXX. figg. 1 and 2).

After this stage the growth in length of tentacles 9—11 of the future spadix becomes arrested while number 12 continues to grow, and thus appears for a time to be the most important member of the confederation, until eventually its limit is reached, the others forge ahead and number 12 retires behind the curtain which grows out from the sheath of number 9 (cf. Pl. LXXX. figg. 7 and 4)[1].

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[1] Van der Hoeven, J., "Bijdragen tot de ontleedkundige kennis aangaande *Nautilus pompilius* L." *Verh. kon. Akad.*, Amsterdam, 1856.

[2] Haswell, W. A., "Note on certain points in the arrangement and structure of the tentaculiferous lobes in *Nautilus pompilius.*" *P. Linn. Soc. N. S. Wales*, (2) x. 1895, p. 544, Pl. 48.

[3] Vayssière, A., *op. cit.*, *Ann. Sci. Nat.* (8) II. 1896.

[4] Willey, A., "In the Home of the *Nautilus.*" *Natural Science*, Vol. VI., June 1895, p. 410. The surface of the hood was white and unpigmented when the specimen was brought to me, but this may have been due to previous discharge of pigment from the epidermal cells of the hood. This often happens when the animals are kept under unfavourable conditions.

[5] This length in an average adult male attains to about 140 mm. I have seen much larger shells of *N. pompilius* from the Moluccan Sea than any that I obtained in New Britain.

The infrabuccal organ of the male consists of a bipartite laminated structure contained in a pouch formed by the integument of the buccal membrane, which in adult specimens projects far back into the peristomial haemocoel (Pl. LXXXII. fig. 3). It was first described and figured by Van der Hoeven[2] (1850) who regarded the lamellae as tentacles modified in a manner similar to those of Owen's laminated organ in the centre of the infrabuccal lobe of the female.

Van der Hoeven's organ (Pl. LXXX. figg. 13—15) has recently been described in some detail by Dr L. E. Griffin[3]. It consists in the adult of a pair of fleshy narrow lobes parallel to one another, closely approximated in the middle line and bearing, upon the outer surface of each about fifteen to nineteen lamellae of which only a certain number are visible in external view, the others being concealed below them like the leaves of a book.

The lamelligerous lobes are united together at the base by an intermediate portion which forms a sort of peduncle, and the adoral surface of lobes and peduncle is beset with the openings of glands, which discharge their secretion into the cavity of the pouch in which the organ is contained (Pl. LXXX. fig. 14). Often in preserved specimens a coagulum is found at the orifice of the pouch. In sections cutting the lamellae at right angles the epithelium clothing the surfaces of the lamellae appears to be richly ciliated, an appearance due, as described by Griffin, to the occurrence of numerous sensory cells bearing sense-hairs.

In a very young male of *N. pompilius*, the smallest specimen which I obtained, the appearance of the infrabuccal organ is different from that which it presents in the adult. Instead of being bent into a U-shape as it becomes at a later stage, the two halves of the gland are extended in the transverse direction with a narrow median tract between the ridges which represent the future lamellae (Pl. LXXIX. fig. 12). The appearance of the infrabuccal organ at this stage suggests that its lamellae are homologous with the tentacles only of the female infrabuccal organ, while the group of lamellae (Owen's "olfactory" organ) between the tentaculiferous lobes is reduced to an insignificant median tract in the male. If this be so, then the infrabuccal organ of the male is not simply homologous with that of the female, but chiefly with the tentacular portion of the latter, the median lamellae of the female organ being mostly suppressed in the male, and the lateral tentacles of the former converted into lamellae in the latter. Apart, however, from the interesting evidence furnished by the development of the male infrabuccal organ, its composition in the adult suggests the same homologies which we may tabulate.

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[1] The spadix of a young *Nautilus* of an age corresponding to that represented on Pl. LXXX. figg. 4—6, has been described and figured by Prof. Vayssière *op. cit.* 1895, Pl. 16, figg. 3 and 4, and Pl. 18, fig. 14.

[2] *Trans. Zool. Soc. London*, Vol. IV. Part 1, 1850, Pl. 8, fig. 9.

[3] *Johns Hopkins Univ. Circ.* XVIII. November 1898, p. 12.

Homologies of Infrabuccal Organ of Male and Female Nautilus.

MALE.	FEMALE.
Lamelligerous lobes	Tentaculiferous lobes
Peduncle	Lamelligerous lobe

I cannot say with certainty whether the innervation of the infrabuccal apparatus of male and female affords conclusive evidence of the truth of the above comparisons, but I think it may.

The first accurate account of the innervation of the female infrabuccal organ was furnished by Mr Graham Kerr in 1895[1]. A single nerve-trunk, the last to leave the pedal ganglion, external to the infundibular nerve (Pl. LXXXII. figg. 4 and 5) crosses the peristomial haemocoel on each side, and penetrates into the base of the infrabuccal organ. "This bends towards the middle line, pursues a curved course in the substance of the lobe, and meets with its fellow of the opposite side" (Kerr, *op. cit.*, p. 676). From this commissural nerve, which I propose to call after its discoverer, *Kerr's collector* or commissure, branches are given off which pass directly to the tentacles and lamellae individually. I have dissected out this remarkable nerve in the female infrabuccal organ, but in the male I have been unable to trace a connection between the right and left infrabuccal nerves, the median portion of the nerve from which, in the female, the branches to the lamellae arise, apparently not occurring in the male (Pl. LXXXII. figg. 1 and 2).

Finally it may be remarked that the infrabuccal apparatus of *Nautilus* in general combines the properties of gland and sense-organ, but that it is in any case an accessory sexual organ since it differs in male and female. It is therefore not appropriate to ascribe an olfactory function to it, since this expression is too precise in the present state of our knowledge and moreover leads to confusion with the true rhinophore[2] and the ophthalmic tentacles which present no sexual differences.

There is another lamellar organ in the female to which I have already referred, which occupies the inner surface of what I have called the ventral symphysial tract. It is composed of two halves separated in the middle line, and the lamellae of each half are disposed in an arcuate manner, running at first longitudinally, and then curving inwards or transversely to the middle line.

This organ was first correctly described by Valenciennes[3], and I shall call it the *Organ of Valenciennes,* in order to distinguish it from the infrabuccal lamellar organ of the female which is the *Organ of Owen,* and from the infrabuccal lamellar organ of the male which is the *Organ of Van der Hoeven.*

The median division which separates the two halves of the organ of Valenciennes is not always very distinct, and Kerr[4] has figured an example in which the lamellae were continued uninterruptedly from one side to the other. Kerr has further found a spermatophore adherent to the lamellae of this organ, thus indicating its function as a *receptaculum seminis.* Curiously enough I have not found a spermatophore in this position in any of my preserved females, but in a living female I once observed the end of a spermatophore protruding from the circumoral complex as shown in fig. 2, Pl. LXXVII. I placed this specimen carefully back into its cage, in the hope of obtaining some result, but nothing came of it.

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[1] Kerr, J. G., *op. cit.*, *P. Zool. Soc. London*, 1895, p. 675.

[2] Owen (1832) surmised that the lamellae of the female infrabuccal organ exercised an olfactory function, in ignorance of the sexual differences which were first made known by Van der Hoeven (1850) and in ignorance of the rhinophore which was discovered by Valenciennes (1841).

[3] Valenciennes, A., *op. cit.* 1841, p. 277, Pl. XI. fig. 1 *t.*

[4] Kerr, J. G., *op. cit.* 1895, *P. Zool. Soc.* Pl. XXXIX. I have also observed that some of the lamellae may become confluent across the middle line, while others in the same organ remain distinct on each side.

On Plate LXXX. figs. 9—12, I have rendered all the secondary sexual characters of a young female, measuring 66 mm. in length from the root of the siphuncle to the anterior border of the hood. The organ of Valenciennes is mapped out but barely laid down, although faint traces of the future lamellae are discernible at the sides. The extrabuccal lobes (Pl. LXXX. fig. 10) exhibit normal development, since they are not specially modified in the female, whereas the infrabuccal lobe shows a retarded development, small in size and with the tentacles just appearing (fig. 11). In conclusion it may be noted, although not coming within the scope of the present chapter, that the *nidamental gland* is only represented by an inconspicuous primordial tract on the inner surface of the ventral mantle-flap (Pl. LXXX. fig. 12).

10. Peristomial Haemocoel; Systemic Aorta; Cephalic Arteries.

The venous system of *Nautilus* consists of definite venous channels, of which the most conspicuous are the vena cava, the pallial veins and the siphuncular vein, of interstitial lacunae and of spacious sinuses. The sinuses are traversed by muscles, nerves, and conjunctive trabeculae, and form vast *cisternae,* surrounding the buccal cone, the crop, and the liver. These three principal divisions of the haemocoel may be distinguished as the peristomial, peri-oesophageal and peri-hepatic haemocoels respectively. They communicate by separate apertures with the *vena cava,* which collects all the blood and transmits it through the central *sinus venosus* and afferent branchial vessels to the gills.

The peri-oesophageal haemocoel communicates with the *vena cava* by means of the numerous fenestrations in the dorsal wall of the latter which were described and figured by Owen (cf. my Pl. LXXXI. fig. 5).

In preserved specimens the liver is often surrounded by an abundant coagulum which conceals the hepatic lobules from view. The wall which shuts off the peri-hepatic sinus from the perivisceral coelom is a thin transparent membrane. The liver, as is well known, consists of right and left portions, and the peri-hepatic haemocoel accordingly opens into the sinus venosus by two orifices which lie mediad of the posterior afferent branchial trunk (which supplies the smaller gill on each side), and dorsad of the genital duct on the right side, and of the pyriform body on the left. These orifices are seen at the back of the sinus venosus after cutting across the rectum which traverses the latter.

The peri-hepatic haemocoel is nevertheless nothing more than a backward prolongation of the peri-oesophageal coelom, protruding like a hernia into the perivisceral coelom. That this is the case may be seen at once by cutting into the haemocoel from the dorsal side, when a forest of slender conjunctive trabeculae are found passing from the inner (mesial) surface of the liver to the wall of the crop.

The peristomial haemocoel is virtually separated from the peri-oesophageal space by a tendinous diaphragm on the dorsal side, and by the tissues and organs of the fundus elsewhere. The diaphragm is a very definite structure stretching from the cerebral capsule to the body-wall in the region of the nuchal membrane (Pl. LXXXI. fig. 7, and Pl. LXXXIII. fig. 26).

The nerve-collar which strictly surrounds the oesophagus is the cerebro-visceral loop. The pedal commissure is separated from contiguity with the oesophagus by an interval which is occupied by the ventral retractor muscles of the buccal mass. The oesophagus passes into the buccal mass precisely at the level of the fundus of the peristomial haemocoel, so that the oesophagus proper lies entirely within the peri-oesophageal haemocoel, the buccal mass[1] with its attendant muscles and nerves being the only portion of the digestive apparatus which occurs within the limits of the peristomial haemocoel.

The cerebral portion of the cerebro-visceral nerve-collar lies within the peristomial haemocoel (Pl. LXXXI. fig. 7) while the visceral portion lies within the peri-oesophageal haemocoel (Pl. LXXXIII. fig. 26). Within the mass of the cephalopodium at the angle of junction of the cerebral and visceral portions of the nerve-collar occur the cephalic organs of special sense (eye, rhinophore, and otocyst) and their nerves. The demarcation of these components of the nervous system is therefore clear.

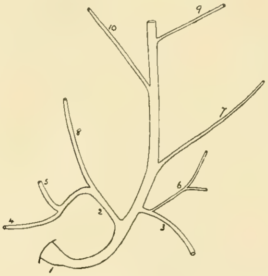

FIG. 8. View of proximal branches of the systemic aorta, from above.

1. Truncus arteriosus (leaving the pericardium).
2. Main hepatic artery.
3. Gastric artery.
4. Right hepatic artery.
5. Left hepatic artery.
6. Posterior proventricular artery.
7. Right posterior columellar artery.
8. Left posterior columellar artery.
9. Right pallio-nuchal artery.
10. Left pallio-nuchal artery.

The greater or systemic aorta of *Nautilus* arises as a large *truncus arteriosus*[2] from the left dorso-posterior region of the heart and leaves the pericardium through the left pericardio-visceral fontanelle. On its mesial side as it leaves the heart it is adherent to the ligament which binds the heart to the floor of the pericardium. Haller (1895) points out that this *cardiac ligament* is a very primitive structure, representing the place of origin of the heart in the coelom.

Having emerged from the pericardium, the great aorta, after a short upwardly directed course through the perivisceral coelom, enters the peri-hepatic haemocoel between the right and left lobes of the liver, and, after a further course of about 15 mm. (in the adult) sends off two important arteries, the *hepatic artery* on the left and the *gastric artery* on the right of the main aortic trunk. It then turns definitely forwards dorsad of the crop, giving off other branches (Text-fig. 8) until it reaches the *intercoelic diaphragm* which separates the peristomial from the peri-oesophageal haemocoel on the dorsal side. Having arrived at this level, the dorsal aorta divides into the two main cephalic arteries which I have formerly called *innominate* arteries. These are the feeders of the peristomial haemocoel.

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[1] There are no extra-bulbar salivary glands in *Nautilus*, but intra-bulbar glands in relation with Owen's faucial follicles have been described by Griffin (*Zool. Bull.* 1897, Vol. I. p. 149, fig. 4). Compare also Joubin, L., "Recherches sur la morphologie comparée des glandes salivaires. Glandes salivaires des Céphalopodes." *Arch. Zool. Expér.* (2) Tome V. Suppl. 1887, Mém. III.

[2] There are simple valves (noted by Owen) at the bases of the branchio-cardiac trunks and a semilunar valve at the root of the *truncus arteriosus*.

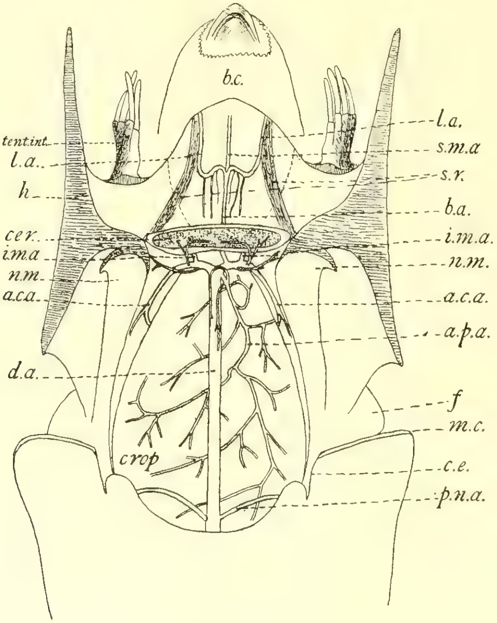

FIG. 9. *N. pompilius*, ♂. Dissection, from above, of the cephalic region to show the cephalic arteries. An incision has been made through the nuchal membrane, the hood, and the buccal membrane. The brain-capsule has been opened, and the median portion of the mantle behind the nuchal region has been removed. *b.c.* buccal cone; *tent.int.* extrabuccal tentacles (the external labial processes of Owen); *l.a.* labial arteries supplying the buccal membrane and fringe; *s.m.a.* superior mandibular artery; *s.r.* superior retractor muscles of the jaws (Owen); *b.a.* buccal artery; *i.m.a.* paired inferior mandibular arteries; *n.m.* nuchal membrane; *a.c.a.* anterior columellar artery; *a.p.a.* anterior proventricular artery; *f.* ala infundibuli; *m.c.* free mantle-edge; *c.e.* cut edge of mantle; *p.n.a.* pallio-nuchal artery; *d.a.* dorsal aorta; *cer.* brain with cerebral arteries; *h.* cut edge of hood.

N.B.—Apart from the cerebral arteries, all the anteriorly directed branches of the innominate arteries pass below the cerebral capsule. [From *Quart. J. Micr. Sci.* Vol. 39, 1896.]

After giving off branches to the buccal mass and to the shell-muscle, the main vessel on each side passes below the cerebral capsule, and follows the inner concave border of the coronal (pedal) ganglion (Pl. LXXXIII. fig. 28). Having arrived at the end of the ganglionic swelling, at the point where the latter passes into the comparatively slender pedal commissure, the vessel passes below or behind the ganglion, and then bends sharply backwards and upwards, sending branches to the tentacles (Pl. LXXXII. fig. 5).

Although too much stress need not be laid upon the vagaries of blood-vessels, yet I think that this recurrent course of the main tentacular arteries may be regarded as an indication of an important transposition of parts or change of topography which has taken place during the evolution of the nautiline plan of organisation.

At the point of flexure of the tentacular artery on each side a large branch is given off which traverses the cartilage and is distributed to the *alae infundibuli*.

In the peristomial fundus there are symmetrically placed apertures leading into various lacunae in the massive cephalopodium; there is one particularly large sinus surrounding the lower portion of the spadix in the male (Pl. LXXXII. fig. 5). The intrabulbar sinuses are of great complexity and I do not propose to analyse them. They are all connected by more or less wide fontanelles with each other and with the peristomial haemocoel.

With regard to the stomatogastric nerves I have nothing to add to Mr Graham Kerr's account, except that the nerves are more deep-seated than his description might lead one to expect. They are below the sheet-like protractor muscle and below all the retractors, and hence it is hardly apposite to speak of them as lying "just below the skin" (Pl. LXXXIII. fig. 29).

The great peristomial haemocoel which is such a remarkable feature in the haemal system of *Nautilus* communicates with the endochondral sinus by two channels which lie between the dorsal protuberances (*arcus cartilaginis*) of the capito-pedal cartilage, and the capsule of the pedal commissure (Pl. LXXXII. fig. 5).

These are the most important fontanelles in the wall of the endochondral sinus, and I propose to name them the *capito-pedal venous orifices.* I have seen a delicate membranous fold on the inner wall of the endochondral sinus arching over the orifice as if it were a valve to prevent the reflux of blood from the sinus to the haemocoel. These are the *capito-pedal valves,* but I cannot certify as to their constant occurrence or effective function though I deem it worth while to direct attention to them (Pl. LXXXIII. fig. 14).

The blood of *Nautilus* when freshly drawn exudes as a colourless fluid which quickly turns bluish at the edges of the fluid mass after exposure to the air, and the bluish tinge gradually advances to the centre. When this has taken place the blood appears of a uniform pale blue colour, which subsequently becomes darker. The blood does not coagulate of itself if left to stand. It contains numerous amoebocytes, which I have sometimes observed both in living and stained preparations to be united together in small groups after the manner of a plasmodium, possibly the result of successive nuclear divisions (Pl. LXXXIII. figg. 1 and 1 *a*). The nucleus of the amoebocytes presents a chromatic network, while the protoplasm appears as a spongy reticulum, containing granules which are dissolved by acetic acid.

11. Reproductive Organs and Genital Arteries.

The constitution and topography of the generative apparatus of *Nautilus* are well known but I will consider them here briefly for the sake of topographical completeness, and to point out the relations in the young, and also because I have formerly[1] described the arteries which are distributed to the glands and ducts direct from the heart.

Owen (1832) stated that the ovary was supplied from the systemic aorta, while Haller (1895) says that it receives branches from what I have called the posterior pallial artery. It is interesting to recall these antagonistic statements concerning the vascularisation of the gonad, since they were both made without apparent misgiving, and are both incorrect. Of course the true facts appear more clearly after injection of fresh material, and it would be quite impossible, I think, to discover the true genital arteries by the most careful dissection of ordinary spirit-specimens.

In young individuals it is evident that the genito-intestinal ligament constitutes the matrix of the gonad, which at its earliest appearance, in my material, is fully formed but of small size, and lies upon and in the right face of the ligament behind the pericardium. This region no doubt corresponds with its seat of origin in still earlier stages, and serves to indicate the primary importance of the genito-intestinal ligament which from an anatomical standpoint represents the true mesentery of the coelom (Pl. LXXX. fig. 20).

In later life, when the gonad has greatly increased in bulk, the anterior portion of the genito-intestinal ligament which is inserted into the pallio-visceral ligament (*i.e.* the perforated septum which separates the pericardium from the perivisceral coelom) appears to be distinct from the rest, and has been named by Haller the genital ligament, but it is not distinct in origin[2].

A narrow offshoot from the genito-intestinal ligament is inserted into the distal wall of the stomach and is the *gastral ligament* (Pl. LXXX. figg. 20 and 23). The proximal end of the stomach, where the oesophagus enters it and the intestine leaves it, is closely adherent to the wall of the peri-hepatic haemocoel (cf. Pl. LXXX. fig. 22).

Anatomical appearances in the young and adult are in favour of the gonad (ovary and testis) of *Nautilus* having arisen as a simple pouch-like invagination of the germinal epithelium into the substance of the primitive mesentery. There is no evidence of secondary formation of a pouch in actual development, and I do not think that the question of the primitive or secondary character of the gonadic pouch from a phyletic standpoint is of great importance. What is of importance is the fact that the gonad lies in the perivisceral coelom, and the sexual products virtually fall into the latter on their way to the exterior. I say virtually, because the coelomic aperture of the gonadic pouch becomes, in the adult, so closely approximated to the coelomic orifice of the genital duct, often actually penetrating into the latter though separate from it, that the ova and spermatozoa are conveyed directly from the gonad to the duct.

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[1] Willey, A., "Letters from New Guinea, etc." *Quart. J. Micr. Sc.* Vol. 39, 1896, p. 172.

[2] Haller (*op. cit.* 1895, p. 202) says:—"Zuvörderst möchte ich mittheilen, dass ich das Genitalligament und zum Theil auch das Genitointestinalligament für zwei solche Doppellamellen halte, die.....................die doppelte Anlage des Cöloms beweisen, da sie meines Erachtens nach die medianen Berührungswände der beiderseitigen Cölomsäcke darstellen. Hier sind somit diesbezüglich noch sehr ursprüngliche Verhältnisse, ähnlich wie bei den Placophoren, erhalten." This is an interesting conclusion, which my observations support except that I find no necessity for qualifying or subdividing the genito-intestinal ligament. It is the one mesentery, and in this capacity it is a morphological unit.

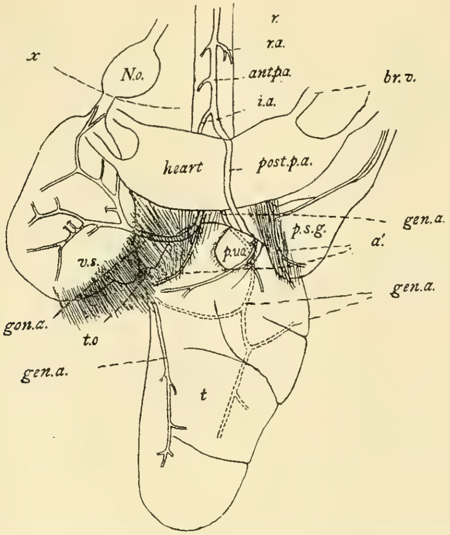

FIG. 10. *N. pompilius*, ♂. Genital arteries from below. *r.* rectum; *r.a.* rectal artery. (N.B.—The rectal arteries are very variable.) *ant.p.a.* anterior pallial artery; *i.a.* intestinal artery. (N.B.—This artery usually passes to the right of the rectum, as shown in this figure; but in one instance I have observed it to pass down to the left of the rectum.) *br.v.* branchial veins; *post.p.a.* posterior pallial artery; *p.s.g.* pear-shaped gland with its artery; *a'.* branches of the preceding artery and of the gonaducal artery, which supply the superjacent ligaments; *gen.a.* genital artery and its branches; *t.* testis; *t.o.* aperture of testis; *p.v.o.* orifice of communication between the pericardial and visceral portions of body-cavity, through which the posterior pallial artery passes; *gon.a.* gonaducal artery; *v.s.* vesicula seminalis. (N.B.—This structure, the testis and pear-shaped gland are closely united to the heart by a ligament.) *N.o.* Needhamian vesicle; *x.* dotted line to indicate where the pallial duplicature merges into the body-wall ventrally. [From *Quart. J. Micr. Sc.* Vol. 39, 1896.]

The main trunk of the median genital artery applies itself at first to the dorsal side of the gonad, and extends round to the ventral side, giving off branches of greater and of lesser importance.

In the female the ultimate ramifications of the genital artery reach the surface of the individual ova, the finer branches following but not confined to the reticulations formed by the ridges of the follicle which project into the yolk (Pl. LXXXIII. fig. 17). The arteries which traverse the surface of the ova (Pl. LXXXIII. figg. 15 and 16), give off minute branches, which pass deeply into the recesses of the follicular ridges and are doubtless the means by which nutriment is conveyed to the vitellus. I noticed that the deep-lying branches anastomose with one another, thus forming a *rete mirabile,* while the superficial branches appear not to form anastomoses.

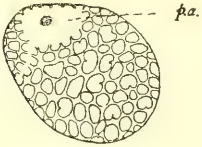

Fig. 11. *N. pompilius.* Fresh ovarian ovum showing the areolation produced by the folds of the egg-follicle which project into the yolk. *p.a.* pellucid polar area, in the centre of which the germinal tract lies.

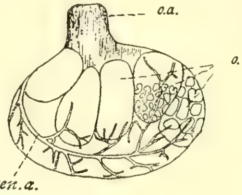

Fig. 12. Ovary of an injected specimen from above. *o.a.* neck of the gonad with orifice at its free end; *o.* ova seen through the transparent capsule of the ovary, with areolations partly drawn to show difference in size of meshes in older (wide meshes) and younger eggs; *gen.a.* dorsal branch of genital artery. [From *Quart. J. Micr. Sc.* Vol. 39, 1896.]

The germinal tract appears in the centre of the clear polar area of the fresh egg as a faint whitish spot upon the ventral aspect of the ova as they lie within the ovary (Text-fig. 13). The older ovarian ova are rendered somewhat shapeless by mutual pressure with a roughly oval outline, and measure 15·5 mm. in length with a maximum breadth of 11·5 mm. When the pressure is relieved by slitting open the ovary the ova round up, and those which are submature have an average diameter of about 10 mm. The yolk is viscous and glutinous with a translucent brownish colour.

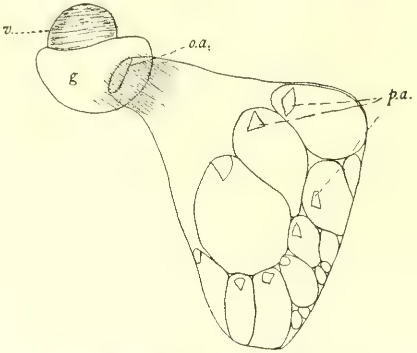

Fig. 13. *N. pompilius,* ♀. Reproductive organs seen from below in fresh condition. *p.a.* polar areas of ovarian ova; *o.a.* orifice of the ovary projecting into the *ostium abdominale* of the oviduct; *g.* uterine portion of oviduct; *v.* vaginal portion of oviduct. [From *Quart. J. Micr. Sc.* Vol. 39, 1896.]

The follicular meshes[1] are close-set in young ova, becoming more open during the later stages of maturation and finally disappearing before oviposition. The nearly ripe ova rupture with the utmost facility, and this may account for certain appearances which have been recorded by Keferstein (1865) and Haller (1895). Keferstein described a large albuminiparous gland (Eiweissdrüse) in connection with the ovary, while according to Haller's interpretation (*op. cit.* p. 199) the ovary is gorged with free yolk in addition to the ova. As I have described above, the vitellus receives its nutriment solely through the vessels of the follicular membrane, and the adventitious occurrence of free yolk can only be ascribed to the rupture of mature or submature ova and is therefore an artefact.

In the female the short oviduct is closely adherent to the wall of the pericardium, and its *ostium abdominale* lies behind and closely apposed to the pallio-visceral ligament.

The male organs of generation have received fresh description on the part of Mr Graham Kerr (*op. cit.* 1895, p. 671), to whose work I may refer the reader, and also to the explanation of the figures 16—19 on my Plate LXXX. The male duct comprises an external and an internal portion. The latter projects boldly into the perivisceral coelom, where it constitutes a *vesicula seminalis* of special composition, consisting of two portions separated from one another by a diaphragm perforated near its mesial border (Pl. LXXX. fig. 17). The *ostium abdominale* leads into the so-called *accessory gland,* which contains a complex lumen in which the spermatophore is fabricated, after which it is passed through a very small aperture into the distal thin-walled portion of the seminal vesicle which I will call the *antrum.* Beyond this point the duct penetrates the integument at the level of the pallial insertion by a narrow neck, and then dilates again to form the so-called *Needhamian sac* which, as described by Van der Hoeven and by Kerr, is partially subdivided into two cavities by an internal longitudinal septum. The septum presents a free anterior border, in front of which the two halves of the cavity unite, and over which the convoluted spermatophore rests as if upon a saddle (Pl. LXXX. fig. 18).

The Needhamian sac is connected with the penis or terminal portion of the *vas deferens* by a narrow neck surrounded by a sphincter. The penis itself is completely divided by an internal longitudinal septum (described and figured by Kerr) so that it contains two lumina, of which only the right is functional and lodges a spermatophore at maturity, the left lumen ending blindly behind.

I have no information concerning the manner in which the spermatophore is conveyed from the penis to its position in the *fossa buccalis* on the dorsal side of the buccal cone, where it is held by the two most dorsally placed tentacles of the extra-buccal series on each side (Pl. LXXVII. fig. 6). The transparent membrane or cyst in which the spermatophore is always contained when it occupies this position is probably secreted by some portion of the spadix.

A mature male will have a spermatophore in the buccal fossa, another in the right penial lumen (which is capable of great distension), and a third in the Needhamian sac. I do not know how the spermatophore is conveyed to the organ of

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[1] The vascular folds of the inner layer of the follicle in the eggs of *Sepia*, noted in their superficial aspects by Kölliker (1844), were first correctly interpreted and described in detail by Lankester, E. R., "Contributions to the developmental history of the Mollusca." *Phil. Trans.*, Vol. 165, 1875, p. 39.

Valenciennes in the female, and I have not been fortunate enough to find a fecundated female among my preserved specimens[1].

I have often taken males which had discharged the spermatophore, the empty and ruptured cyst remaining behind in its usual position in the *fossa buccalis*. In captivity the males sometimes become sperm-bound, that is over-mature, the spadix presenting a congested appearance and the penial lumen and Needhamian sac turgid with spermatophores, death resulting.

12. Mechanism of Respiration; Branchiae and Osphradia; Renal and Pericardial Follicles.

The pallial insertion of the gills of *Nautilus* has been already referred to. They are planted upon the mantle by means of a thick, fleshy peduncle which serves as a massive buttress at the back of each gill, *i.e.* on the venous side of the gill (Pl. LXXXII. fig. 8). The inner surface of the gill, that is to say, the side which is turned towards the middle line of the body, is the arterial surface, and the vessel which lies below this surface leads directly into the corresponding *branchio-cardiac* or efferent branchial trunk. The outer surface, which is supported by the above-mentioned buttress at the base of the gill, is the venous surface, and the vessel which lies below the integument on this side is the continuation of the corresponding *reno-branchial* or afferent branchial vessel which arises from the *sinus venosus*.

In *Nautilus* as in other Cephalopoda, and moreover as in the Diotocardia (*Haliotis*, *Pleurotomaria*, etc.) and in the Acephala, the renal apparatus is intercalated into the branchial circulation.

The structure of the gill of *Nautilus* strongly resembles that of the gill of the Gastropoda, Prosobranchia, Diotocardia, Aspidobranchia. It consists of an axis or stem bearing a double series of alternating branchial *folia* or gill-plates, and only differs in details from the gills of other Cephalopoda[2]. Especially does it agree with the latter, and diverge from the prosobranchiate gill in the absence of cilia from the branchial epithelium[3]. The stem of the gill of *Nautilus* arises by a broad but simple peduncle from the inner surface of the mantle not far from the angle of insertion of the mantle into the body-wall, and it undergoes no secondary concrescence either with the mantle or with the body-wall, being free from base to apex. Each branchial lamella is attached to the stem by means of a supporting membrane which presents a free border on the dorsal (venous) side of the gill. The free borders of the basilar membranes of the branchial lamellae are strengthened by a pair of subcutaneous deeply staining skeletal bars which appear to contain scattered cellular elements, but are not like true cartilage, resembling rather a thickened basement-membrane. The skeletal bars may be called the *gill-bars,* and each branchial folium[1] contains a pair of them. The proximal ends of the gill-bars, where they pass into the substance of the stem, are united together in couples so as to form U-shaped prongs in such a way that the two limbs of the fork pass into consecutive gill-plates.

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[1] A spermatophore released from its cyst and adhering to the organ of Valenciennes was first figured by Mr Graham Kerr (*op. cit.* 1895). Another instance has quite recently been recorded by Mr L. E. Griffin in a work which was received at the British Museum too late for extended and critical notice here. Griffin, L. E., "The Anatomy of *Nautilus pompilius*," *Mem. Ac. Washington*, Vol. VIII. fifth memoir, pp. 103—197, 11 text-figg. 17 plates, dated 1898 on cover, 1900 on title-page, received at the British (Natural History) Museum on March 24th, 1902.

[2] Cf. Joubin, L., "Structure et développement de la branchie de quelques Céphalopodes des côtes de France." *Arch. Zool. Expér.* (2) III. 1885, pp. 75—150, Pl. IV.—VI.

[3] In *Haliotis* for example the whole surface of the branchial lamellae is ciliated (Wegmann, *Arch. Zool. Expér.* (2) II. 1884, p. 316). The gill-primordia are ciliated in *Loligo* according to Brooks (*Anniv. Mem. Boston Soc. Nat. Hist.* 1880), but not in *Sepia* according to Kölliker (*Entwick. d. Cephalopoden*, 1844, p. 54).

Leaving out of consideration the gill-lamellae of the Acephala, a strictly comparable skeletal apparatus has been found to exist in the prosobranchiate Gastropods and in the dibranchiate Cephalopods.

In *Haliotis,* Wegmann (*op. cit.* 1884, p. 316) says that an attentive examination of a branchial folium shows that its venous border is much more resistant than its arterial border. The former is rigid and sharply defined, the latter soft and undulating, the difference in consistency of the two borders being due to the existence, along the venous border, of an internal skeleton consisting of a hyaline stylet which attenuates towards the apex of the lamella.

In *Sepia,* Burne[2] has described a series of branchial cartilages consisting of slender rods (one to each gill-plate) standing out from the branchial gland (which occupies the stem or septum of the gill) and stiffening the free basal edge of each supporting membrane. The cartilage of which the rods are composed agrees in structure with the other cartilages of the body, *i.e.* branching cells imbedded in an abundant hyaline matrix.

In *Pleurotomaria* each ctenidium[3], according to the careful description furnished by the late Martin Woodward[4], consists of a stout axial septum bearing two sets of triangular gill-plates. The gill-plates are strengthened by a pair of supporting rods along their outer (*i.e.* venous) margins. These rods resemble those which I have found in *Nautilus* in being flattened structures closely applied to the epidermis and enclosing between them portions of the blood-space of the gill-plate. They lie along the dorso-lateral borders of the gill-plates, and arch round from one plate to the next at the dorsal attachment of the plates to the gill-septum.

It will be seen that Woodward's account of the gill-bars in *Pleurotomaria* might be applied almost word for word to the corresponding structures in *Nautilus.*

The course of the blood through the gills has been described by Joubin[5], who has noted the absence of capillaries.

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[1] An entire branchial folium consists of the branchial lamella proper and the basilar membrane by which it is attached to the stem of the gill.

[2] Burne, R. H., "On some points in the anatomy of *Sepia officinalis* L. II. On the presence of a series of cartilages in the branchiae." *P. Malac. Soc. London,* 1899, Vol. III. pp. 53—56, text-figg.

[3] This is the term introduced by Professor Lankester for the true molluscan gill as distinguished from other adventitious respiratory structures in certain Mollusca and from the gills of other animals.

[4] Woodward, M. F., "The anatomy of *Pleurotomaria beyrichii* Hilg." *Quart. J. Micr. Sc.,* Vol. 44, 1901.

[5] Joubin, L., "Recherches sur l'appareil respiratoire des Nautiles." *Rev. biol. Nord France,* II. pp. 409—428, Pl. VII. 1890. The branchial gland of Cephalopoda is regarded by Joubin as a blood-producing gland giving origin to amoebocytes, therefore a kind of lymph-gland. He describes groups of cells (called in German "Lymphheerde") in the stem and peduncle of the gill of *Nautilus.* I have also seen in the region of the gills and osphradia and also in the siphuncle groups of large cells with reticular protoplasm which may be lymph-glands.

When an *Octopus* is observed at rest, attached by its suckers to a surface, its violent respiratory movements are seen to depend upon the muscularity of the mantle and funnel. the expansion of the mantle being synchronous with the contraction of the funnel, so that while fresh sea-water is entering the mantle-cavity in order to bathe the gills, water which has completed its work of oxygenation is being expelled through the funnel. In the case of *Nautilus* the thin transparent mantle is closely applied to the inner surface of the mouth of the shell, and takes no part in promoting the respiratory current of water. The incurrent and excurrent streams are alike caused by the rhythmic contractions of the funnel, more particularly of the *alae infundibuli.*

This is an interesting difference between the mechanism of respiration in *Nautilus* and Dibranchs respectively, and was noted by me in 1896 (*Quart. J. Micr. Sc.* Vol. 39) in correction of a statement by Moseley, who attributed breathing-movements to the mantle[1]. The funnel of *Nautilus* is thus the essential organ of locomotion and the principal accessory organ of respiration, a combination of functions which should not be dissociated from its anatomical structure and relations when its morphology is under discussion[2].

It is not my intention to describe in detail the renal and pericardial follicles which adhere respectively to the anterior and posterior walls of the afferent branchial vessels, the former enclosed within the renal sacs and the latter projecting into the pericardium.

The pericardial glands discharge a fluid excretory product into the pericardium, which has been met with as a tenacious coagulum by Keferstein (1865) and Haller (1895), but I have no record of this. The excretion of the renal glands, as is well known, consists of solid concretions with concentric stratification somewhat as in starch-grains (Pl. LXXVI. fig. 2). They are said to consist mainly of phosphates (Blasius, Keferstein). When seen in bulk, filling the cavities of the renal sacs, their colour varies from white through scarlet to deep crimson (cf. Pl. LXXV. and LXXVI. fig. 1). I can suggest no explanation of this variation in colour of the excretory products. The colour is retained in many of my alcoholic specimens.

A dissection displaying the afferent and efferent vessels of the larger gill of the right side is represented on Pl. LXXXII. fig. 8, to the explanation of which I may refer the reader.

Both the renal and the pericardial follicles are contractile in their entirety, the systole of the heart synchronising with the diastole of the pericardial glands and with the systole of the renal organs[3].

With regard to the branchial sense-organs or *osphradia* which are highly characteristic of Gastropoda and Pelecypoda (Lamellibranchs), *Nautilus* affords a most interesting link between the Cephalopoda and these two groups.

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[1] Moseley, H. N., *Notes by a Naturalist on H.M.S. Challenger*, 2nd edit. 1892, p. 257. "On either side ....the fold of mantle closing the gill cavity was to be seen rising and falling, with a regular pulsating motion, as the animal in breathing took in the water, to be expelled by the siphon." The "fold of mantle" is really the *ala infundibuli.*

[2] The mechanism of respiration of the Cephalopoda was dealt with in an instructive and suggestive manner by Williams, T., "On the mechanism of aquatic respiration and on the structure of the organs of breathing in invertebrated animals. Cephalopoda." *Ann. Nat. Hist.* (2) xix. 1857, pp. 193—201, Pl. xv. He points out the analogy between the contractile gills of Cephalopoda and the systole and diastole of the lungs in pulmonary respiration.

[3] I also observed rapid independent contractions of the renal organs.

It appears that in the dibranchiate Cephalopoda there are no osphradia[1], and it is probable that they have been lost in correlation with the much higher development of the cerebro-visceral nervous system in these forms as compared with *Nautilus.*

There are two pairs of osphradia in *Nautilus*, one to each gill. The fact of the existence of branchial sense-organs in *Nautilus* was first made known by Lankester and Bourne in 1883, and the pair described by them is that which corresponds with the lesser gill on each side. It appears as a small arcuate papilla between the bases of the gills; the sensory surface is below the arch (cf. Pl. LXXXIII. figs. 6—8).

The second pair of osphradia appears as a quadrilobate papilla, often referred to as the post-anal papilla, because it occurs behind the anus when the mantle is drawn back. This compound papilla obviously consists of two bilobate papillae which have coalesced in the middle line, though the degree of coalescence varies considerably, and occasionally they are quite separate. In freshly captured specimens I soon became convinced of the homodynamy[2] of these papillae with the osphradial papillae of Lankester and Bourne, and eventually recognised the fact that the deep fissure which causes the bilobate appearance of the former corresponds with the angle made by the arch of the latter with the wall of the mantle, and that in both cases the sensory epithelium was provided with vibratile cilia, and was practically destitute of the gland-cells which are so abundant elsewhere (Pl. LXXXIII. figg. 3—8).

In the light of the preceding facts, more especially after the discovery of cilia on the protected surfaces of both pairs of osphradia, I decided in my own mind that the osphradial nature of the "post-anal papilla" was established, and I had seen traces of small nerves branching out towards the osphradia from the main visceral nerves (cf. Pl. LXXVIII. fig. 1), though I had not ascertained their mode of termination in the sensory epithelium. Pelseneer has recently denied that the "post-anal papilla" is innervated from the visceral nerves. He says[3]: "Qu'il n'y a pas non plus de fibres nerveuses allant de ces nerfs à la papille postanale elle-même, et que celle-ci n'est pas un organe sensoriel, comme le supposait Willey. L'extrémité de ces nerfs viscéraux médians innerve seulement le manteau et, chez la femelle, la glande nidamentaire."

Again on p. 58 of his work Pelseneer refers to the "Papilla postanale" in these words:—"Ainsi qu'il a été dit plus haut, elle ne reçoit pas de nerf important; elle ne présente, ni sur elle ni autour d'elle, aucune région sensorielle. Son assimilation à une seconde paire d'osphradies fusionnées [Willey] ne parait donc pas soutenable." Dr Pelseneer makes no reference to my discovery of cilia[1] on the osphradia, otherwise he could hardly have been so categorical as to the absence of a "région sensorielle."

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[1] The cephalic sense-organ consisting of a "small antero-posteriorly directed ridge, which is placed below and a little behind each eye," described by Mr W. E. Hoyle as the "osphradium" in *Gonatus fabricii* (*P. Zool. Soc. London*, 1889, p. 125), obviously corresponds with the rhinophore of *Nautilus*. The osphradium is often or usually described as an olfactory organ, but the term is limited to the branchial sense-organs, to which it was first applied by Professor Lankester (Article "Mollusca," *Encyc. Brit.*).

[2] This homodynamy was also indicated by Van der Hoeven, although he was ignorant of their osphradial nature. He says (*Tr. Zool. Soc. London*, Vol. IV. Part I. 1850) on p. 24:—"Behind the anus [with reflected mantle] there are on each side two small and depressed caruncles very similar to that mammillary eminence or papilla we have seen at the root of the first branchia."

[3] Pelseneer, P., "Recherches morphologiques et phylogénétiques sur les Mollusques archaïques." *Mem. Cour. Ac. Belgique*, t. LVII. 1899, p. 57 (Reprint).

Continued investigation of the organs by finer methods than I had previously employed has resulted in a confirmation of my interpretation (Pl. LXXXIII. figg. 3—8). Even without this confirmation I should have confidently adhered to the view expressed upon grounds of topography, homodynamy, and ciliation of protected surfaces, and I gather that this view has found favour with Dr Ludwig Plate[2].

The two pairs of osphradia may be distinguished as the *interbranchial osphradia* and the *submedian*[3] *osphradia* respectively. The nerves which supply the former are not difficult to find in section, and they have been figured in longitudinal section, *i.e.* in a section parallel to the sagittal plane of the body, by Pelseneer (*op. cit.* Pl. XXI. fig. 180). Pelseneer says that the papilla is not sensory, but only the subjacent pallial epithelium, which receives "un grand nombre de ramifications d'un filet du nerf viscéral-branchial." I am able to confirm this statement, with the reservation that I find that the sensory epithelium is not confined to the adjacent pallial surface, but extends round the angle of insertion of the papilla (Pl. LXXXIII. fig. 7).

In the case of the submedian osphradia the entire sensory epithelium is raised above the level of the pallial surface while maintaining its character as a sensory groove, for protective purposes no doubt, and so it comes about that the papillae are bilobate with the sensory surface occupying the depression between the lobes in each case. The nerves are best seen in sections taken parallel to the long axis of the body, and in such sections, if properly prepared, the nerves may be found to penetrate through the basement-membrane of the epidermis, and to spread out in the substance of the latter external to the basement-membrane (Pl. LXXXIII. figg. 3—8). In this way a remarkable *intra-epidermal fibrillar plexus* is brought into existence comparable for example with the intra-epidermal terminations of the collar nerve-roots of the Enteropneusta[4]. What is more to the point however is that an exactly similar intra-epidermal distribution of nerve-fibres in the osphradia was described by Professor Spengel[5] in 1881 in the case of the primitive Lamellibranch *Arca noae* as well as in the Prosobranchs *Haliotis* and *Trochus*. The identity of distribution of nerves in the osphradia of these Molluscs and of *Nautilus* may be said to be demonstrative.

According to Professor Spengel's account, the osphradium of *Arca* resembles that of *Haliotis* and of *Trochus* in that from the subjacent visceral ganglion numerous nerves arise which enter the pigmented cylinder-epithelium and distribute themselves in this "so dass wir dasselbe eigenthümliche Bild einen von starken Nervenfasersträngen durchbrochenen Epithelschicht vor uns haben wie dort."

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[1] Willey, A., "The pre-ocular and post-ocular tentacles and osphradia of *Nautilus*." *Quart. J. Micr. Sc.* Vol. 40, 1897, pp. 197—201, Pl. x.

[2] Plate, H. L., "Die Anatomie und Phylogenie der Chitonen." Fortsetzung Fauna Chilensis, Part C. *Zool. Jahrb.*, Supplement v. Bd. II. 1901, p. 561.

[3] The epithet "post-anal" in this connection is wrong both in substance and in fact.

[4] Cf. *Zool. Res.*, Part III. 1899, especially the case of *Ptychodera carnosa*, p. 252.

[5] Spengel, J. W., "Die Geruchsorgane und das Nervensystem der Mollusken. Ein Beitrag zur Erkenntnis der Einheit des Molluskentypus." *Zeitschr. wiss. Zool.* Bd. 35, 1881, p. 375, Taf. XIX. fig. 27.

In the sensory epithelium of the osphradium of *Nautilus* I have seen cells with large vesicular nucleus and darkly staining nucleolus, bearing a great resemblance to ganglion-cells, and as I have found them in special relation with the nerves it seems very probable that they are in fact peripheral ganglion-cells which have retained their primitive position in the epidermis. They are best seen in tangential sections (Pl. LXXXIII. fig. 5).

13. EYE; RHINOPHORE; OTOCYST.

I do not propose to dwell in detail upon these structures but to focus attention, for the special purpose of this contribution, upon their topography. They are in fact inextricably involved in the cephalopodium, and it is of the utmost importance to appreciate their character of true cephalic sense-organs, whereas the ciliated ophthalmic tentacles between which the eye is placed belong to the digital series.

The eye of the *Nautilus* is a hollow hemisphere with an opaque pigmented cornea perforated near the centre by a small aperture which is the pupil of the eye. The size of the pinhole aperture is apparently capable of slight accommodation to the intensity of light as I have seen it contract from a comparatively wide orifice, 2·5 mm. in diameter, to a mere slit with apposed margins. Passing from the aperture to the ventral border of the eye is a superficial pigmented groove somewhat resembling a choroid fissure or raphe. Perhaps the development of the eye would throw some light upon the meaning of this corneal raphe.

The dorsal border of the eye is convex, but the rest of the margin is produced into a thin limbus. Sometimes the corneal raphe commences a short distance below the pupil, and the latter then appears as an isolated subcentral orifice.

The eye faces outwards and cannot be moved in any other direction, the optic peduncle being relatively immobile and capable only of slight protraction. The whole aspect of the pedunculated eye somewhat resembles a sheath of a digital tentacle, and Macdonald[1] actually asserted that there can be little doubt that the eye is a modified tentacular sheath so fashioned as to become the seat of the special sense of vision. There is perhaps no obvious inherent impossibility in this view, especially when regarded from the standpoint of those who consider the digital tentacles to be special cephalic processes, but I think it is important to dismiss the idea from the mind if it should ever present itself.

The eye of *Nautilus* was correctly described in respect of the pinhole aperture and absence of dioptric apparatus by Owen (1832), and was subsequently examined in greater detail by Hensen[2] (1865). Later still it was shown by Fraisse[3] to represent a primordial type of eye which is also met with among the prosobranchiate Gastropods.

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[1] Macdonald, J. D., "Further observations on the anatomy and physiology of *Nautilus*." *P. R. Soc. London*, VIII. 1857, pp. 380—382. In this connection the fact may be mentioned that the optic peduncle does not contain an axial nerve but separate nerves arise from the ganglion and pass through the eye-stalk to the retina.

[2] Hensen, V., "Ueber das Auge einiger Cephalopoden." *Zeitschr. wiss. Zool.*, Bd. XV. 1865. *Nautilus*, p. 203, figures on Taf. XIX. and XX. Later notes have been furnished by Haller, *op. cit.* 1895.

[3] Fraisse, P., "Ueber Molluskenaugen mit embryonalem Typus." *Zeitschr. wiss. Zool.* Bd. 35, pp. 461—477, Taf. 25—26.

The eye of the limpet (*Patella*) resembles that of *Nautilus* upon a very small scale and bears a similar relation to the tentacle (allowing for changes in proportion and in topography) to that which the eye of *Nautilus* does to the rhinophore. The latter remark applies with even greater force to the much larger eye of *Haliotis* (cf. my Pl. LXXVI. fig. 5), in which the cornea is likewise perforated, though the chamber of the eye is filled by a vitreous body (Fraisse).

The eye of *Pleurotomaria* as described and figured by M. F. Woodward (*op. cit.* 1901) also resembles in principle the eye of *Nautilus*, the cornea being perforated, while the cavity of the optic cup is only partially filled by the vitreous body.

In *Nautilus* the vitreous body is represented by a clear bacillary layer (Stäbchenschicht) overlying the pigmented retinal epithelium, but it does not extend over the inner surface of the cornea, which therefore appears as a black disc with the pupil in the middle when seen from the inside (Pl. LXXXIII. fig. 25).

The extremely limited movements and accommodation of the eye of *Nautilus* suggest that in spite of its size it is a photometric or photoscopic organ rather than a visual organ.

The rhinophore was discovered by Valenciennes (1841). It consists of a small papilliform tentacle placed below the eye, with an aperture at its base leading into a deep pit lined by a ciliated epithelium, which is thrown into low folds. From the depth of the pit and the difficulty attending its dissection the designation *olfactory labyrinth* seems to be justified (Pl. LXXXI. fig. 6).

The otocyst was discovered by Macdonald (1855). It lies over but not in the posterior cornu of the cartilage and immediately external to the coronal ganglion, so that it has to be turned aside in order to expose the latter from the outside (Pl. LXXXI. fig. 6, and Pl. LXXXII. fig. 6). It contains in the fresh condition a milky substance, which is so fluid that one experiences a certain difficulty in procuring some of it for examination, so readily does it trickle away from the ruptured otocyst. Under the microscope it resolves itself into a vast number of minute calcareous bodies called *otocones* (Pl. LXXXIII. fig. 2). These were correctly described by Macdonald, but sometimes the contents of the otocyst harden in alcohol into a coagulum which has occasionally given rise to the erroneous impression that the otocyst of *Nautilus* contains a single otolith.

The eye and rhinophore of *Nautilus* apparently correspond with the eye and tentacle of *Haliotis* or *Strombus* for example. Nevertheless this simple comparison has not always been evident since Dr Pelseneer[1] in his work on the morphology of the arms of Cephalopoda failed to grasp this relation, and apparently ignoring the existence of the rhinophore[2] claimed the ophthalmic tentacles of *Nautilus* as the representatives of the typical molluscan cephalic tentacles and stated that they are innervated by the supraoesophageal ganglion.

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[1] Pelseneer, P., "Sur la valeur morphologique des bras et la composition du système nerveux central des Céphalopodes." *Arch. Biol.* VIII. 1888, see p. 730.

[2] Although he refers to the "nerf olfactif" in a footnote.

14. THE MOLLUSCAN FOOT.

The foot of a Gastropod in its fullest development consists of a median sole[1] and lateral appendages resembling metapleural folds.

Huxley (*Phil. Trans.* 1853) divided the median portion of the foot into three portions, *propodium, mesopodium, metapodium,* and called the lateral portion the *epipodium.* He pointed out that of all Mollusca the Heteropod genus *Atlanta* possesses the best developed foot-proper, and has its parts best specialised and separated, the peculiar ciliated sucker of this pelagic animal representing the mesopodium.

Twenty years later Grenacher established a more fundamental subdivision of the molluscan foot, retaining Huxley's epipodium, but viewing the entire median portion, whether simple or differentiated into regions, as the *protopodium*[2], which is not to be confused with Huxley's propodium.

Huxley's threefold subdivision of the protopodium still remains, though of subordinate importance. An interesting example of it is afforded by the widely distributed species *Harpa ventricosa,* which I met with in the course of my travels. In this form the protopodium as a whole is capable of enormous extension so as to cover a relatively immense superficial area, and the propodium is not only marked off from the rest of the foot by a deep notch on each side, but Brock[3] has discovered that it possesses a special innervation in the form of a very remarkable nervous reticulum. The mesopodium and metapodium of *Harpa* appear at a hasty glance not to be differentiated from one another as there is no operculum, but closer inspection reveals a line of division between them, and if the hinder or caudal end of the foot of the living animal be held firmly in the hand the metapodium is cast off and remains in the hand while the animal falls to the ground. This is an interesting example of muscular autotomy which was known and is referred to in the *Cambridge Natural History*[4], though the suggestion that it is effected by pressure of the shell is erroneous (Pl. LXXVI. fig. 3).

The metapodium is cut off with a clean concave anterior surface, the posterior surface of the mesopodium after the act of autotomy being convex. There is no effusion of blood.

In a large species of *Oliva* which was common at Lifu, the protopodium is also capable of great extension and will wrap itself round land-snails which are offered to it as bait by the natives.

The sides of the protopodium may be produced into great natatory folds as in Aplysiidae. These lateral expansions of the protopodium are called *parapodia* (Pelseneer) or *pteropodia* (von Jhering). Whether or not these are of the nature of true epipodia is a question which does not concern us here.

The epipodia are presented in their most typical development in certain prosobranchiate genera, particularly in *Haliotis,* where they appear as a pair of deeply cleft pleural folds bearing tentacles on their margins. Anteriorly the two borders of each epipodium merge together, and the single tentaculiferous lobe encroaches in a very singular manner over the dorsal side of the mouth between the latter and the cephalic tentacles. There is also a nuchal membrane which arches over the head in front (Pl. LXXVI. figg. 4 and 5).

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[1] The "foot-proper" of Huxley.

[2] Grenacher, H., "Zur Entwickelungsgeschichte der Cephalopoden. Zugleich ein Beitrag zur Morphologie der höheren Mollusken." *Zeitschr. wiss. Zool.*, Bd. 24, 1874, see p. 465.

[3] Brock, J., "Zur Neurologie der Prosobranchier." *Zeitschr. wiss. Zool.*, Bd. 48, 1889, pp. 67—83, Taf. 6 and 7.

[4] Cooke, A. H., "Molluscs." *Cambr. Nat. Hist.*, Vol. III. 1895, p. 45.

When the protopodium presents a flat or plantar surface of reptation as in *Haliotis* and most Gastropoda I shall speak of it as a *platypodium*. The platypodium is therefore to be defined as a plantar protopodium.

The Cephalopoda and the prosobranchiate Gastropoda agree in so many features of organisation that a definite relationship between them seems to be highly probable. Perhaps the most fundamental difference lies in the absence of a plantar foot in the Cephalopoda.

In a subsequent chapter I shall endeavour to show that the cephalopodium of *Nautilus* is of epipodial origin, while the siphonopodium represents the protopodium alone.

It is true that there is a discussion among malacologists concerning the true nature of the epipodium, some authorities, foremost amongst whom is Dr Pelseneer, maintaining the view of its *pedal* origin, whilst M. Boutan[1] is in favour of its *pallial* origin, and calls it the "manteau inférieur." I would, however, derive the cephalopodium of *Nautilus* from a primitive epipodium wholly irrespective of any morphological interpretation which may be put upon the latter.

I may nevertheless suggest or rather repeat a suggestion which is implied in a paragraph of Huxley's work (1853, p. 50)[2] that the epipodium is a pleural fold of the body-wall, and perhaps should be discussed independently of the foot as well as of the mantle.

In the work of comparing *Nautilus* with other Mollusca, but especially with a Gastropod like *Haliotis*, everything depends upon the interpretation of *pallial*, *pleural*, and *pedal* derivatives, or in other words, we have to ascertain the relations and modifications of the typical molluscan mantle, epipodium, and protopodium respectively.

15. CHANGES OF FUNCTION, ORGANS AND TOPOGRAPHY.

The doctrine of Change of Function (Functionswechsel) was, I think, first raised to the rank of a morphological principle by Dr Anton Dohrn in 1875. The development of organs by substitution or "Organwechsel" was first made the basis of a principle by Kleinenberg in 1886. I am not aware that the phenomenon of translocation of organs has been hitherto utilised for the purpose of establishing a principle of "Change of Topography" which should have equal value with the other two in morphological inquiry. The three principles may operate severally or in combination. Both change of function and substitution of organs are often found associated with more or less radical changes of topography.

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[1] Boutan, L., "Le système nerveux du *Parmophorus* (*Scutus*) dans ses rapports avec le manteau, la collerette (manteau inférieur) et le pied." *Rev. biol. Nord France*, II. 1890, pp. 449—478, Pl. VIII. and IX.

[2] Huxley says the bilateral archetype of the Mollusca corresponds with the vertebrate and articulate archetypes. "The appendicular system of the Vertebrata and Articulata is represented by the epipodium in the Cephalous Mollusca."

One of the simplest examples of change of topography is to be met with in connection with the position of the vent in Teleostean fishes, even in closely allied species. Instances of this kind (as also in regard to the position of the pelvic fins of fishes) are exceedingly numerous, but one of the most striking cases has been brought to my knowledge by the courtesy of Mr G. A. Boulenger, F.R.S. In the Berycid genus *Trachichthys* the vent is placed normally behind the series of abdominal scales, but in the closely allied genus *Paratrachichthys* "as first observed by Günther, the vent is far forward between the ventral fins, in front of and not, as usual, behind the series of abdominal scales[1]."

I have selected this example of change of position of the vent, because the antero-posterior axis of many animals corresponds more or less closely with what has been called the *oro-anal axis*; it does so for example in the most primitive group of Mollusca, the Amphineura (*Chiton*, *Chaetoderma*, *Neomenia*). In consequence of this circumstance the oro-anal axis has frequently been adopted as a fixed quantity, from which all bearings must be taken. This may be true in special cases but it is clearly not true for the Cephalopoda, at least this is my opinion of the matter, and I do not regard the antero-posterior axis as synonymous with the oro-anal axis, although, as indicated above, I do not forget that the two may coincide.

In *Nautilus* and the Cephalopoda generally, in consequence of the flexure of the intestine there is no longer any question of an oro-anal axis, but there is an antero-posterior axis which it is our business to discover.

The evidence of change of topography in *Nautilus* based upon anatomical conditions is to be traced directly in the occurrence of conflicting axes, and in the existence of recurrent nerves and arteries, and indirectly in the relations of the siphuncle. With regard to the conflicting axes I am aware that these are visionary allies, since they involve an imaginary interpretation of imaginary lines, but I have come to the conclusion that what I have to say is not destitute of possible interest.

The capito-pedal cartilage, the skeletal basis of the body of *Nautilus*, possesses a distinct longitudinal axis of its own, and this axis does not coincide with the axis of the cephalopodium, but describes an angle with it[2] (Pl. LXXXI. figg. 1 and 2).

It seems a possible view to take that the *skeletal axis* may represent the primitive longitudinal axis of the uncoiled ancestor of *Nautilus*, that the tilting of the *cephalopodial axis* is evidence of the concrescence and translocation of the primitive *epipodium* (the tentacles of *Nautilus* being here regarded as epipodial tentacles), and finally that the ventral *pallial flexure* of *Nautilus* has resulted in the formation of a visceral sac or abdomen, which lies chiefly below the level of the primitive antero-posterior axis (Pl. LXXXI. fig. 2). The lateral portions or cornua of the cartilage which determine the direction of its main axis, occur along the angle of junction of the epipodium (cephalopodium) and protopodium (funnel).

The recurrent nerves of the posterior ophthalmic tentacles obviously indicate change of primitive topographical relations of parts, and perhaps a similar interpretation, although not so certain, may be put upon the recurrent tentacular arteries (Pl. LXXXII. fig. 5, and Pl. LXXXIII. fig. 28).

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[1] Boulenger, G. A., "Notes on the classification of Teleostean Fishes. II. On the Berycidae." *Ann. Nat. Hist.* (7) IX. 1902, p. 203.

[2] These relations are best seen in dissections of relaxed specimens.

With regard to the siphuncle, while it is certain that it has a physiological relation to the air-chambers of the shell, its morphological nature is not so clear, but I think it is a vestige, a vermiform appendix of *Nautilus*, the remnant of the primitive elongate body which we must suppose the remote ancestor of *Nautilus* possessed. The gut and the coelom have vanished from the siphuncle, and it is now reduced to the condition of a vascular appendage, of vital importance to *Nautilus* in a physiological sense, but a mere vestige morphologically.

16. Flexure and Orientation.

When squids are watched darting through the water with their pointed hinder extremities turned in the direction of locomotion, the possibility of there being any question concerning the orientation of the animal, *i.e.* concerning the true bearings of the antero-posterior axis, never occurs to the observer. It is left to the refinements of morphology to raise such a question, the discussion of which is only too apt to be profitless and uninteresting. It is however impossible to neglect it in a work like the present.

Considered as Mollusca, the problem of the orientation of the body of Cephalopoda depends upon and is created by two main features of organisation:—(1) the absence of a plantar foot or platypodium; (2) the ventral position of the forwardly directed anal aperture, which is associated with what Huxley (1853) called a neural flexure of the intestine.

The current notions regarding the orientation of a Cephalopod follow the lines laid down by Huxley, according to whom the visceral sac represents a dorsal hump or abdomen while the arms represent a ventral foot, so that the morphological position of the animal is taken to be that which is sometimes assumed for example by *Octopus* (cf. also my Pl. LXXVII. fig. 3) in which the arms are directed downwards, *i.e.* towards the substratum and the visceral sac upwards. This is also the position which is usually postulated for *Nautilus* on the tacit assumption that *Nautilus* in spite of its possession of many primitive anatomical characters, affords no fresh clue in this regard.

Another view with which I find myself, under certain reservations, in substantial agreement, has been started in recent years by Dr B. Haller. I may quote the following paragraph from this author's work on *Nautilus* (*op. cit.* 1895, p. 191): "Bezüglich der Orientirung möchte ich vorausschicken, dass ich den *Nautilus*, wie überhaupt die Cephalopoden (wie ich dies ausführlicher schon mitgetheilt habe[1]………) aus einem chitonartigen Mollusken so hervorgegangen mir vorstelle, dass letzterer mit seinem hinteren Körperabschnitt sich von hinten nach vorn und somit nach ventralwärts bog, wodurch……… der After nach vorn zu gelangte………Vorn ist der Kopf, hinten der Sipho."

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[1] Haller, B., "Studien über docoglosse und rhipidoglosse Prosobranchier, etc." Leipzig, 1894, p. 149. The "Sipho" means of course the siphuncle.

In the course of the following pages I shall give my own reasons for regarding the cephalopodium of *Nautilus* as being anterior in position and (far from being ventral) having a marked dorsal inclination by which, as mentioned above, its main axis as determined by the direction of the sheaths of the digital tentacles has become tilted at an angle with the skeletal axis (Pl. LXXXI. figg. 1 and 2)[1].

With regard to the flexure or coiling of the external, multilocular, involuted shell of *Nautilus*, it was noted by Huxley (1853, p. 49) that the direction in which it is wound is the same as that in which the intestine is bent, so that if the coils of the shell be imagined free as they are in *Spirula*, the convexity is dorsal and the concavity ventral. This method of coiling has been called exogastric by Owen[2], while the shell of *Spirula* which is coiled in the reverse direction is endogastric. *Spirula* is a coiled Belemnite (Valenciennes), *Nautilus* a coiled *Orthoceras* (Owen), and *Ammonites* a coiled *Baculites* (Owen).

The shell of *Nautilus* is external and protective, it is an involute cone of great length, and its length increases *pari passu* with the growth of the animal until the latter reaches its specific cubic capacity or limit of growth. The deposition of septa and secretion of gas convert the shell into a hydrostatic apparatus.

Owen regarded the straight chambered shells of fossil Cephalopoda as having been produced by the progressive unwinding of a coiled shell and the evidence seems to point in this direction.

If this be so, then the origin of the shell is lost in the remotest antiquity, and it is useless to discuss the question whether the arthrocochlid (von Jhering) shell-system of the Polyplacophora (*Chiton*) has any possible relation to the septate shell of the primitive Cephalopoda.

The actual facies of *Nautilus* is determined by its visceral flexure, and by its pedal and epipodial topography, and this is therefore the place to refer to a question which has been raised by Dr Plate[3], namely, as to whether the siphonopodium (Schwimmfuss) of Cephalopoda is derived from a platypodium or *vice versâ*. It seems to me that the direct answer to this question depends entirely upon one's individual proclivities. The cleft funnel of *Nautilus* conveys the impression of a platypodium, with the margins folded over each other in a manner recalling that in which the large extensile foot of certain Gastropods (*Harpa, Oliva*, etc.) is capable of wrapping itself round foreign objects.

If we imagine the body of *Nautilus* to be straightened out and the anus carried back to its primitive terminal position, the dimensions of the primitive platypodium, extending from end to end of the body, may appear appalling. It is however quite conceivable that the enormous bulk of the Cephalopods, as a whole, was correlated with the achievement of the peculiar relations of the animals to their shells, and therefore came into being subsequently to the evolution of the plan of composition of the Cephalopod organisation.

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[1] I may also refer the reader to the two preceding chapters.

[2] Owen, R., "On the relative positions to their constructors of the chambered shells of Cephalopods." *P. Zool. Soc. London*, 1878, pp. 955—975, Pl. 40.

[3] Plate, H. L., *op. cit.* 1901, p. 559.

The siphonopodium seems to be a more highly specialised organ than the platypodium, and for this direct reason in combination with collateral considerations, it is probably more useful at present to accept the dogma that the foot of the molluscan archetype was a platypodium.

17. Morphology of the Tentacles of Nautilus.

The two theories of the special nature of the tentacles of *Nautilus*, considered merely from a cephalopodan standpoint, have been referred to in a former chapter, and may be tabulated in chronological order as follows:—

1. Acetabular Theory of Valenciennes (1841), according to which a tentacle of *Nautilus*, consisting of the *sheath* and the *cirrus*, is homologous with a sucker of a Dibranch consisting of *cupule* and *caruncle*.
2. Branchial Theory of Owen (1843), according to which a tentacle of *Nautilus* is homologous with an arm of a Dibranch.

Both of these theories have received authoritative support, and neither of them is to be lightly rejected, since neither is capable of such final proof as would satisfy the higher criticism.

The independent innervation of the individual tentacles of *Nautilus*, the demonstration of their definite *suctorial ridges* by which they are enabled to adhere to surfaces with great tenacity, and the virtual identity of their internal structure with that of a true arm, weigh so heavily, to my mind, on the side of the Branchial Theory, that I must follow Owen in admitting their equivalence with the arms of the Dibranchs just as the multitudinous legs of a Myriapod are individually equivalent to the legs of a Hexapod insect. It was further suggested by Owen that the inner whorl of the cephalopodium of *Nautilus* may be represented in the decapod Calamaries and Cuttle-fishes by the two long retractile prehensile arms or anchors, which are provided at the base with a kind of sheath.

It is worth repeating that the suctorial ridges of *Nautilus* actually tend to become semilunar or half-cup-shaped towards the apices of the outermost tentacles, a feature which is especially noticeable in the ophthalmic tentacles. Nevertheless it is quite possible that a single ridge does not correspond with a single sucker, but rather with a transverse row of suckers such as occurs in *Gonatus*, where the arms carry four series of suckers[1]. A curious analogy is afforded by the second and third tentacles of the spadix in *Nautilus*, the transverse costae of the former being represented by the transverse rows of *alveoli* in the latter (cf. Pl. LXXIX. fig. 9).

In support of the Acetabular Theory of Valenciennes it is of great historical interest to know that the case of *Cirroteuthis* was quoted by Johannes Müller at a meeting of the Berlin Academy on the occasion of the communication by Humboldt of an abstract of the results achieved by Valenciennes in his work upon the anatomy of *Nautilus*[2]. Johannes Müller is reported to have said that the *Cirroteuthis* of Eschricht has arms which are not furnished with suckers but with delicate filiform tentacula, but the fact is that there is a median row of suckers as in *Eledone,* though the suckers are reduced, and alternating with them are 26 pairs of cirri on each arm[1].

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[1] Cf. Hoyle, W. E., *op. cit. P. Zool. Soc. London*, 1889.

[2] *Bericht Akad. Berlin*, 1841. Bemerkungen des Hrn. Prof. J. Müller, p. 58. Translated in *Ann. Nat. Hist.* Vol. VII. 1841, pp. 241—245.

When we come to consider the broader interpretation of the arms of Cephalopoda from a pan-molluscan standpoint we are again confronted with two rival theories which may be defined as follows:—

1. Pedal Theory of Huxley[2] (1853), according to which the arms of Cephalopoda are derivatives of the primitive molluscan foot.

2. Cephalic Theory of Leuckart (1848) and von Jhering (1877), according to which they are special appendages and derivatives of the primitive head.

The most complete exposition of the Pedal Theory is contained in the memoir by Pelseneer[3], while the Cephalic Theory has been strongly advocated by Grobben[4], and more recently by Kerr[5].

Huxley, as is well known, regarded the arms of Cephalopoda as representing the protopodium and the funnel the epipodium[6]. "The formation of an abdomen," he said, "with a peculiar development of the margins of the foot into elongated processes, and with cohesion of the posterior epipodial lobes, gives us the Cephalopodan subtype." From this quotation it is clear that Huxley considered the arms as marginal appendages, which is in itself an important conclusion. His reason for identifying them with the protopodium may possibly be looked for in the bionomical fact that *Octopus,* for example, actually does crawl about from place to place by means of its arms, although it can swim vigorously on occasion. The identification of the funnel with the epipodium may be due to the fact of the cleft funnel of *Nautilus,* the flaps of which may be likened to pteropodial lobes.

Grenacher (*Zeitschr. wiss. Zool.*, Bd. 24, 1874) homologised the arms with the velum of Gastropod embryos, but adopted Huxley's interpretation of the funnel on account of the development of the latter from paired primordia.

The special reasons for the view that the funnel is an epipodial derivative are therefore based upon facts of bionomics, comparative anatomy, and embryology, but I believe that these are facts which mask the truth in this particular case. The epipodium as the name implies lies dorsad of the protopodium, while the siphonopodium of Cephalopods is ventral in position, and although great allowances may be made for changes of topography it is difficult to admit the probability of such a complete *situs inversus*, nor is it necessary in order to co-ordinate the facts.

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[1] Eschricht, *Cirroteuthis mülleri*; *Nova Acta Ac. German.* t. 18, 1836, p. 627, tabb. 46—48. "Octopus suctoriis minimis unam seriem in quovis brachio formantibus; brachiis cirratis et cum membrana natatoria ......usque ad apicem fere connatis."

[2] Huxley, T. H., "On the morphology of the cephalous Mollusca as illustrated by the anatomy of certain Heteropoda and Pteropoda collected during the voyage of H.M.S. Rattlesnake in 1846—50." *Phil. Trans.* Vol. 143, 1853, pp. 29—65.

[3] Pelseneer, P., "Sur la valeur morphologique des bras.........des Céphalopodes." *Arch. Biol.*, VIII. p. 723, 1888; see also Dr Pelseneer's "Report on the Pteropoda." *Chall. Rep.*, Part 66, Vol. XIX. 1888. Anatomy (Part III. of Report) Chapter II. "Are the Pteropoda Cephalopoda?" p. 60.

[4] Grobben, C., "Morphologische Studien über.........Cephalopoden." *Arb. Inst. Wien*, v. 1884, see p. 222 (p. 44 of *Separat. Abd.*). Also Grobben, C., "Zur Kenntniss der Morphologie und der Verwandtschaftsverhältnisse der Cephalopoden." *Arb. Inst. Wien*, VII. 1886, pp. 60—82.

[5] Kerr, J. G., *op. cit.* *P. Zool. Soc. London*, 1895, see p. 678.

[6] Huxley, T. H., *op. cit.* 1853, Pl. v. fig. 5, p. 51.

The only author who has referred to the possibility of the epipodial origin of the cephalopodium, so far as I know, is Professor Brooks[1], and he adopts a somewhat pessimistic attitude in the matter. Professor Brooks commences his remarks by referring to what may be defined as the Velar Theory of Lovén (1848) and Grenacher (1874), by whom the arms of Cephalopoda were compared with the velum of other molluscan embryos, but it cannot be said that this theory has enjoyed a great measure of success, and Brooks has found that in *Loligo*, at the stage at which the ingrowth of the stomodoeum takes place, the rudiment of a true velum appears on each side of the mouth in the form of a faintly marked, undulating, ciliated band arising near the corners of the mouth, and extending laterally to the eye-stalk, crossing the outer ventral edge of the latter. The position of this line, its relation to the mouth and the eye-stalk, and the presence of cilia upon it, are all indications that it represents a true velum.

Professor Brooks adds that "the siphon originates as two pairs of folds[2] . . . . and if we regard these four folds as homologous with the epipodial folds of a Gastropod, the arms must be regarded as independently acquired structures. If we regard the arms as modifications of the epipodial folds we must consider the four siphon folds as independently acquired structures[3], and as we have nothing whatever to furnish us with a test, nothing seems to be gained by the uncertain homology of either the arms or the siphon, with any part of the body of a typical Gastropod."

On the other hand I think it will be no mean gain for morphology if we can secure the recognition of the epipodial nature of the arms and the protopodial nature of the funnel of Cephalopoda, and the longer I meditate upon the subject the safer do these homologies appear to my mind. It is, as everyone knows, a difficult matter to adduce a clinching argument in favour of a theoretical conclusion, and if the cumulative weight of what has been brought forward in the preceding pages is not sufficient to turn the scale, I fear it will be impossible to say more with advantage.

The following is a summary of the special grounds upon which I base my Epipodial Theory:—

1. Tentacles of *Nautilus* regarded as marginal appendages.
2. Sequence of the tentacles of *Nautilus* and of their nerves.
3. Topography of cephalopodium and siphonopodium, the dorsal position of the former, the ventral position of the latter, and the deep longitudinal *pleural raphe* which separates them.
4. Comparison with *Haliotis* where we find in schematic disposition, mantle, epi-

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[1] Brooks, W. K., "The development of the squid, *Loligo pealii* (Lesueur)." *Anniv. Mem. Boston Soc.* 1880, 22 pp., 3 Plates.

[2] These folds clearly correspond with the anterior *crura infundibuli* and the posterior *alae infundibuli* of the funnel of *Nautilus*.

[3] This is equivalent to saying, what I believe to be true, namely, that the method of development of the funnel from paired primordia, is a *cenogenetic* feature in the embryos of Cephalopoda which may be correlated with the special adaptation of the protopodium which has resulted in the formation of the funnel and with the abundance of yolk in the eggs of Cephalopoda, in which respect *Nautilus* surpasses all other known genera.

podium and platypodium, these structures being represented in *Nautilus* by the mantle, cephalopodium and siphonopodium respectively.

5. The recognition of a dorsal and a ventral symphysis or lines of concrescence in the cephalopodium of *Nautilus*.
6. The relation of the cephalic sense-organs to the cephalopodium of *Nautilus* and their homology with the corresponding organs in Gastropoda.
7. The presence of an outer and an inner whorl of tentacles in the cephalopodium of *Nautilus* in apparent correspondence with the double nature of the tentaculiferous epipodium of *Haliotis*.
8. The presence of the funnel-organ which according to Jatta represents a pedal gland.
9. The position, form and relations of the capito-pedal cartilage of *Nautilus*.

A word may be added by way of justification for the attempt to construct the above theory in the absence of embryological evidence. The enormous size of the vitellus of the egg of *Nautilus* renders it highly probable that the development of the tentacles and funnel would be direct, it would take place *in situ*, and the topography of the adult would be maintained in the embryo, all special embryonic events, although of the greatest possible interest in themselves, being of a cenogenetic nature[1]. I have actually observed that the inner whorl of the cephalopodium arises in a perfectly direct manner (Pl. LXXX. figg. 1 and 2).

The following tabular view of the principal theories relating to the arms of Cephalopoda will at once illustrate the complexity, interest, and importance of the subject.

Author	Cephalopodium	Siphonopodium	Valve	Funnel-organ	Protopodium
Huxley	Protopodium	Epipodium	——	——	Arms
Grenacher......	Velum	Epipodium	——	——	Wanting
von Jhering...	Cephalic tentacles	Pteropodium	Protopodium	——	Valve
Lankester......	Propodium	Mesopodium	Metapodium	——	Arms + Funnel + Valve
Brooks	Neomorph	Neomorph	Neomorph[2]	——	Yolk-sac
Grobben	Cephalic captacula (as in *Dentalium*)	Epipodium	Protopodium	——	Valve
Pelseneer	Protopodium	Epipodium	——	——	Arms
Jatta............	——	——	——	Pedal gland	Arms + Funnel
Kerr	Cephalic processes	Protopodium	——	——	Funnel
Willey	Epipodium	Protopodium	Neomorph[2]	Pedal gland	Funnel

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[1] This does not refer to the development of the shell and siphuncle, which is likely to afford many instructive data. Even with regard to the cephalopodium important facts might be ascertained regarding the concrescence of the pleural folds.

[2] In *Loligo* the valve develops at a late stage as an outgrowth from the inner wall of the funnel (Brooks). When seen from the inside of the funnel with the flaps of the latter turned aside (cf. my Pl. LXXXIII. fig. 27) the free border of the valve is seen to be concentric with the anterior border of the funnel. Between

Should the foregoing inferences appeal to malacologists in general, an important deduction relating to the homologies of the nervous system remains for consideration. It would follow that the coronal[1] ganglion and commissure of *Nautilus* and their outgoing nerves are equivalent to the *pleuro-pedal system* of prosobranchiate Gastropods, and that here, as in *Nautilus*, the central and peripheral nervous apparatus is composed of two principal systems in close union with one another by means of connectives, but otherwise distinct, namely, the *cerebro-visceral system* and the *pleuro-pedal system*.

18. Diplomerism of Nautilus.

There are indications of two distinct metameres in the trunk of *Nautilus*, and the demonstration of the osphradial nature of the "post-anal papillae" adds another link to the chain.

Owing to the visceral flexure of the mantle which involves renal organs, gills, rectum, etc., in other words, owing to topographical readjustments occasioned by life within a shell[2], the segments do not occur entirely in metameric succession, but the morphologically anterior segment lies ectad and dorsad of the morphologically posterior segment, and even behind the latter. A representation of the two segments is contained in the figure on Pl. LXXV., which shows the pallio-visceral region of *Nautilus* seen from below through the transparent mantle during life, with natural colours.

In order to avoid repetition of the terms "anterior" and "posterior" now in a morphological, now in a topographical sense, I will call the morphologically anterior segment the outer or *microbranchiate segment*, since it comprises the lesser gill; the morphologically posterior segment is the *macrobranchiate* or submedian segment.

I. Microbranchiate segment contains on each side of the body:—

1. The smaller branchia.
2. A reno-branchial vessel, to which are appended
3. The outer pericardial gland, and
4. The outer renal organ which lies in
5. The outer renal chamber which opens to the exterior by
6. The outer renal orifice.
7. The posterior branchio-cardiac vessel.
8. Outer pericardial ligament (Pl. LXXXII. figg. 7 and 8).
9. Interbranchial (outer) osphradium.
10. Outer viscero-branchial nerve.
11. Outer viscero-osphradial nerve.
12. Generative orifice on right side and orifice of pyriform body on the left.

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the valve and the dorsal wall of the funnel there is a deep angle or groove and it seems possible to compare this with the anterior *sulcus* which characterises the border of the propodium in *Harpa* (Pl. LXXVI. fig. 3), *Pleurotomaria* (Woodward) and other prosobranchiate Gastropods. This sulcus is the "glande pédieuse antérieure" or "sillon du bord antérieur du pied" (Pelseneer, *Introd. à l'étude des mollusques*, 1894, p. 52).

[1] Generally called "pedal."

[2] Or accompanying it.

II. Macrobranchiate segment contains on each side:—

1. The greater branchia.
2. A reno-branchial vessel, to which are appended
3. The inner pericardial gland, and
4. The inner renal organ which lies in
5. The inner or submedian renal chamber which opens to the exterior by
6. Its own renal orifice.
7. The anterior branchio-cardiac vessel.
8. The inner (anterior) pericardial ligament.
9. The inner or submedian osphradium.
10. Inner viscero-branchial nerve.
11. Inner viscero-osphradial nerve.
12. The viscero-pericardial orifice.

The outer visceral nerve supplies both of the gills and the interbranchial osphradium. The inner visceral nerve supplies the mantle (nidamental gland in female) and the submedian osphradium.

The heart of *Nautilus* has undergone a semi-rotation by which the origin of the systemic aorta is carried backwards and the positions of the branchio-cardiac vessels permanently inverted, the anterior pair draining the greater (morphologically posterior) branchia, while the posterior pair is associated with the lesser (morphologically anterior) branchia.

The diplomerism breaks down in a somewhat puzzling fashion when we come to consider the coelom, since the pericardium and the perivisceral coelom can hardly be regarded as homodynamous subdivisions of the secondary body-cavity. There is therefore no true coelomic metamerism in *Nautilus* in spite of the existence of metameric abdominal pores, namely, the generative and viscero-pericardial orifices, the latter at any rate taking the place of the *nephrostomes* of other Cephalopoda[1].

An interesting, analogous, physiological interrelation between *nephrostomes* and *abdominal pores* has been established by Bles[2] in fishes.

19. AFFINITIES.

I do not propose to undertake an exhaustive discussion of the affinities of *Nautilus* beyond what has been already said. With regard to the relationship of *Nautilus* and Cephalopoda in general to the Amphineura, the most primitive of existing Mollusca, in which the antero-posterior axis coincides with the oro-anal axis, I will refer the reader to the works of Kerr, Haller, and Plate to which I have already referred[3].

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[1] Cf. Jhering, H. v., *Zeitschr. wiss. Zool.*, Bd. 35, 1881. Grobben, C., *Arb. Inst. Wien*, v. 1884 and vii. 1886. Kerr, J. G., *P. Zool. Soc. London*, 1895. Ziegler, H. E., "Über den derzeitigen Stand der Cölomfrage." *Verh. Deutsch. Zool. Ges.* 1898, p. 14.

[2] Bles, E. J., "Abdominal pores and nephrostomes in fishes." *J. Anat. Physiol.*, Vol. xxxii. p. 484; also *P. R. Soc. London*, Vol. 62, 1898, p. 232.

[3] See further Kerr, J. G., "Phylogenetic relationship between Amphineura and Cephalopoda." *Zool. Anz.*, xxiv. 1901, p. 437.

It is difficult to know how to regard the Aplacophora (*Neomenia, Chaetoderma*), but as for *Chiton* itself, the constant octomerism of the shells seems to indicate that it is a highly finished type which has retained primitive relations of main axis and bilateral symmetry.

Kerr holds that the Amphineura are the nearest living allies of the Cephalopoda, and he gives instructive diagrams of their coelomic properties. In respect of the mutual relations between coelom and haemocoel, *Nautilus* is particularly interesting, and in respect of its possession of a spacious perivisceral coelom incompletely divided into two halves by a median mesentery, the genito-intestinal ligament, *Nautilus* seems to present a more primitive organisation than any other existing mollusc.

Grobben (1884–1886) was of opinion that the Scaphopoda (*Dentalium*) were the nearest living allies of Cephalopoda, but this view has not been sustained by Simroth in his most recent treatise on the former group in Bronn's *Thierreich.*

For my part I have found, during a somewhat limited experience of malacological matters, that a comparison of *Nautilus* with the prosobranchiate Gastropods, more especially with *Haliotis,* seems to throw considerable light upon the organisation of the former genus and indirectly of the dibranchiate Cephalopods.

The torsion of the pallio-visceral region of *Haliotis* with the correlated streptoneurism of the visceral commissure, in spite of the profound effect it has had upon the facies of the animal, may be regarded from a morphological standpoint as an incidental phenomenon equally with the pallio-visceral flexure of *Nautilus.*

If abstraction be made of the torsion of *Haliotis* and the flexure of *Nautilus* the general resemblance between the two genera can be more readily conceived, and the relation of the Cephalopod to the Gastropod would appear in the same light as that which a Hexapod insect bears to a Myriapod, or a Decapod Crustacean to a Phyllopod.

If we take into consideration the analogous phenomena of cephalisation in different groups of coelomate animals, it becomes evident that the general tendency is to evolve a composite head and a concentrated central nervous system. In this sense the *cephalopodium* of the most highly organised group of Mollusca is analogous with the *cephalothorax* of a crab or a lobster. There is thus undoubtedly a *prima facie* case for the composite nature of the cephalopodium, tending to exclude the idea that this structure can be merely a derivative of the head without the co-operation of any part of the trunk.

I have endeavoured to show that *Nautilus* presents certain features of organisation which have become obliterated in the Dibranchs, but which are of crucial significance in regard to the interpretation of the organisation of Cephalopoda, and this without regard to the diplomerism and perivisceral coelom of *Nautilus.* Chief among these nautiline characteristics, I reckon the remarkable tilting of the cephalopodial axis at an angle to the skeletal axis (Pl. LXXXI. fig. 1). If this is a sound description of facts it must be of importance in itself, and especially because no such conflicting axes can be observed in the Dibranchs. I interpret it as meaning that a tentaculiferous epipodium has coalesced with the head and grown round the buccal cone both above and below, while the protopodium has suffered a greatly inferior modification of structure, simply having its margins folded over to form a funnel.

In the commonly accepted orientation of Cephalopoda, no difference is recognised between *Nautilus* and Dibranchs, and *Nautilus* is not specially consulted in the matter, and yet I think it is alone a competent witness.

The similarities between *Nautilus* and a diotocard Prosobranch (*Haliotis, Fissurella, Pleurotomaria*), whether of the nature of affinity or of convergence, include the following points.

SYSTEM.	TETRABRANCHIATA.	PROSOBRANCHIATA.
Circulatory.	*Aorta inferior s. pallialis.*	*Arteria pallialis.*
	Aorta superior s. systemica.	*Truncus arteriosus communis.*
	Intestinal branch of pallial artery.	Rectal branch of pallial artery.
	Reno-branchial system.	Similar.
	Peristomial haemocoel.	Cephalic sinus.
Nervous.	Pleuro-pedal collar.	Pleuro-pedal cords.
	Intra-epidermal fibrillar plexus of osphradium.	Same.
Sensory.	Eye with perforated cornea.	Same.
Motor.	Cephalopodium.	Epipodium.
	Siphonopodium.	Platypodium.
Branchial.	Branchial folia biserial.	Same.
	Branchial skeleton.	Same.
Pallial.	Nidamental gland.	Hypobranchial gland (Haller, 1894).
Reproductive.	Dioecism.	Same.
Digestive.	Pyloric coecum.	Similar.
	Ciliated intestinal epithelium.	Same.
	Absence of extrabulbar salivary glands.	Same.

With regard to the relationship of *Nautilus* to the other Cephalopoda opinions will always differ as to details, but the main issues are clearly defined. In respect that it is a Cephalopod, the external shell of *Nautilus* is probably primitive as compared with the internal shell of *Spirula* and the other Dibranchs[1].

Upon the primitive characters of the digestive system, the paired liver, structure of pyloric coecum, etc., Haller (1895) may be consulted. Brock tabulated upwards of a dozen different combinations and correlations of oviducts and nidamental glands, and pointed out that the slit-like orifices of the renal sacs of *Nautilus* are of primitive significance, inasmuch as this kind of renal orifice is again met with in all Oigopsid cuttle-fishes, and in the more primitive forms of the other subdivisions, whereas in the higher Myopsidae and Octopoda a fleshy renal papilla has developed[2]. He thinks that the Octopoda are the most highly specialised Cephalopoda (as illustrated in the structure of the central nervous system, the eye which can be closed by eyelids, the atrophy of the shell), but that they retain many primitive features such as the crop, the septum between the renal sacs, the paired oviducts.

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[1] On vestigial shells of Cephalopoda see Appellöf, A., "Über das Vorkommen innerer Schalen bei den achtarmigen Cephalopoden (Octopoda)." *Bergens Mus. Aarbog.* 1898, No. 12.

[2] Brock, J., "Studien über die Verwandtschaftsverhältnisse der dibranchiaten Cephalopoden." *S. B. Soc. Erlangen*, 1879, Heft 11, pp. 114—141. Also *Morph. Jahrb.*, VI. 1880, p. 185.

20. FOOD; MIGRATION; PROPAGATION.

The specimen of *Nautilus* which was dissected by Owen contained fragments of triturated Crustacea in its stomach and crop, and this would seem to constitute its staple food-supply since prawns and crabs abound on the nautiline terrains.

As mentioned in a previous chapter any kind of animal bait will tempt *Nautilus*, and after a full meal the crop is found to be gorged to repletion.

In order to be in a position to form a just estimate of the value of the various accounts and legends concerning the habits of *Nautilus* several facts require special consideration. In the first place Owen drew attention to the circumstance that whereas two kinds of *Nautili* are referred to by Aristotle, only one kind is mentioned by Pliny. In his *Thesaurus Conchyliorum*, Sowerby (1855) took care to note particularly that the Pearly Nautilus is not the *Nautilus* of Pliny, which is *Argonauta* or the Paper Nautilus, so-called on account of the thin, white, delicate structure of its peculiar shell.

No doubt many of the fantastic ideas concerning our *Nautilus*, more especially such as possess the popular mind, owe their origin to a simple confusion between the Pearly or, as we may picturesquely term it, Aristotle's *Nautilus* and the Paper or Pliny's *Nautilus*. That this is the case is indicated in a convincing manner by the identity of some of the myths which have been related in connection with both species[1].

It is also desirable to remember that *Nautilus* obviously draws its supplies of food from the bottom of the sea, it is a ground-feeder, while *Argonauta*, according to available evidence, is a pelagic feeder.

When *Nautilus* has been taken, as a great rarity, at the surface of the sea, it has generally, if not always, been found that the specimen was in a more or less moribund condition. At the same time, with its known faculty for swimming and migration in some places into quite shallow water a few fathoms only in depth, it is quite conceivable that an individual specimen might occasionally wander away from its home and arrive at the surface, but there is no evidence that this is a regular practice.

In his "Notes by a Naturalist on H.M.S. Challenger," Moseley also gives it as his opinion that "it is probably a mistake to suppose that it ever comes to the surface voluntarily to swim about."

Moreover only single individuals have ever been seen at the surface and then in the daytime[2], but the evidence of the traps goes to show that *Nautilus* is a gregarious animal and nocturnal in its habits. It repairs in shoals at night to its shrimping grounds, but I suspect that it breeds in deep water or in inaccessible submarine gullies.

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[1] On the subject of the legendary accounts of the habits of *Argonauta*, the following interesting paper may be consulted:—"Observation d'un Argonaute de la Méditerranée," by H. de Lacaze-Duthiers, *Arch. Zool. Expér.* (2) x. 1892, pp. 37—56, with figure of the animal in swimming attitude on p. 41.

[2] *E.g.* Saville-Kent, W., "Preliminary observations..................in connection with the surveying cruise of H.M.S. Myrmidon at Port Darwin and Cambridge Gulf." *P. R. Soc. Queensland*, VI. p. 229, 1888.

In his account of the specimen of *Spirula* obtained by Sir Edward Belcher during the voyage of H.M.S. Samarang 1843—1846, Owen (Zoology of the "Samarang," London, 1850, *Mollusca*, p. 6) called attention to the fact that the two known genera of existing polythalamous Cephalopods were noted for the extreme rarity of the entire animal as compared with the frequency of the shells in collections of Natural History. In the remaining Report on the Mollusca of the "Samarang," Messrs Arthur Adams and Lovell Reeve recorded the fact that no living *Nautilus* was seen during the whole course of the expedition, although it was assiduously sought for.

There is not much to be added here concerning the propagation of *Nautilus*. Some animals breed freely in confinement, others become egg-bound, and others again lay sterile eggs, as *Nautilus* did in my cages. I obtained some evidence that the captivity had the effect of interfering with the normal intercourse of the sexes. On one occasion in particular I had been keeping a male (in which owing to an injury to the hood the spermatophore in the buccal recess protruded at the surface as in Pl. LXXVII. fig. 5) under careful observation for several days. Eventually the spermatophore was discharged from its cyst, and I found it lying on the floor of the cage.

This is what inclines me to believe that it is necessary to work with a large installation, a specially fitted-up aquarium of large size with concrete walls, in order to rear the embryos of *Nautilus* successfully. I have no doubt that the shell and several chambers are formed while the embryo is still in the egg-capsule, and that the young *Nautilus* hatches out with the general facies of the adult.

I tried artificial fertilisation without success, and I do not think it is practicable. The very young shell which is in all probability formed within the egg-capsule has been called the *nepionic shell*, and may be easily recognised by its colour and finer grain in young shells, being separated from the subsequent shell-substance by a well-marked suture, which is visible in the umbilicus of the shells of *N. macromphalus* and *N. umbilicatus*.

The clear brown vitellus of the egg is surrounded by viscid colourless albumen which accumulates at the poles. Between the yolk and the albumen there is a delicate hyaline *vitelline membrane*. The vitellus is larger than that of any other known Cephalopod.

When the females reach maturity, the bilabiate vagina and the nidamental gland become enlarged, protuberant, and turgid, and the edge of the shell is thickened. The nidamental gland frequently assumes a greenish colour. Thus a female *N. pompilius* with submature ovarian ova had a moderately developed, yellow-coloured nidamental gland which had not become turgid. In another of the same age the yellow gland was tinged with a greenish colour. In another the sub-turgid nidamental gland was of a dull greenish or yellowish-green colour. In a nearly mature female the nidamental gland had a pronounced green colour. Apparently the gland does not always turn green, as I have recorded instances of nearly mature females in which it exhibited a rich cream-yellow coloration, the largest ovarian ova, in such specimens, attaining a length of 17·6 mm. and a maximum breadth of 15 mm.

The organ of Valenciennes also becomes turgid and functionally active with abundant secretion of mucus at maturity.

The eggs of *N. pompilius* differ very slightly from those of *N. macromphalus*[1], and like the latter they are laid singly. The pectinate ridges are more prominent on the outer capsule of the egg of *N. pompilius*, often having a frill-like appearance and projecting freely for a short distance at their anterior ends.

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[1] Willey, A., "The oviposition of *Nautilus macromphalus*." *P. R. Soc. London*, 1897, Vol. 60, pp. 467—471, 6 figg.

The capsules of the egg are often deficient in some respects, sometimes exposing the vitellus through the gaping sutures of the inner capsule (Pl. LXXXIII. fig. 18), and in the case of *N. macromphalus* at Lifu I frequently found fully formed capsules without any contents, the latter not having escaped, but never having been present. This also must I think have been due to a derangement of the normal reflexes, the result of captivity. The pectinate ridges of the outer capsule of the egg seem to correspond with the annulations of the infrabuccal tentacles (Pl. LXXIX. figg. 2 a and 6 a).

For further details concerning the egg-capsules I may refer to the explanation of figures 19—23 on Plate LXXXIII.

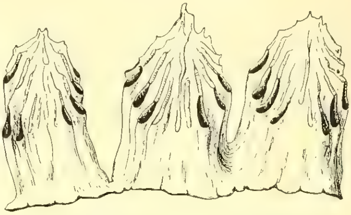

Fig. 14. Three eggs of *N. macromphalus* laid in a row, with capsules coalescent.

21. Variation and Regeneration.

Although the old idea of the fixity of species has long been superseded, the fixity of certain types seems to be a fact not open to question. Fixity of type is the expression of a completed evolution, and this is what is meant when a particular type is said to be highly specialised in a given direction. Fixed types are very likely the same as persistent types, and they have some properties in common amongst which are their limited range of variation and their defective power of regeneration.

The variation in the number and disposition of the digital tentacles of *Nautilus* is a negligible quantity, but the spadix exhibits ambidextral variation, being now on the left side of the cephalopodium and now on the right. A variation of a similar nature affects the origin of the main siphuncular artery, which sometimes arises as a branch of the left division of the posterior pallial artery and sometimes from the right division. The constitution of the spadix shows hardly any appreciable variation.

In one instance only did I meet with a *situs inversus* of the reproductive apparatus, and this was the case with a male in which the *vas deferens* was developed on the left side instead of on the right, with the pyriform gland on the right instead of the left side (Pl. LXXVIII. fig. 2).

More than once or twice I found males in which the hood had been so bitten away that the spermatophore lodged in the buccal recess was exposed to view. Sometimes the front part of the hood is eaten away, at other times a piece is bitten out of the middle of the hood just over the spermatophore (Pl. LXXVII. figg. 5 and 6).

At first I attributed these injuries to the attacks of voracious fishes, but it is not impossible that they are the results of nuptial combats. Without in any way relaxing its hold upon the shell, *Nautilus* can project its body from the shell with a darting movement and protrude the buccal cone so as to seize hold of its food. I have seen it seize a prawn between its jaws in this way, and it would not be a difficult matter for a female to bite into the hood of a male. However this may be, the point to which I desire to draw attention is that the wounds heal up at the edges, but the parts are not regenerated.

TABLE OF VARIATIONS.

	Sex	Spadix	Siphuncular artery	Colour of Renal Concretions
1.	♂	Sinistral	Sinistral	
2.	„	Sinistral	Sinistral	
3.	„	Dextral	Dextral	
4.	„	Sinistral	Sinistral	
5.	„	Sinistral	Dextral	
6.	„	Sinistral	Dextral	
7.	„	Sinistral	Dextral	
8.	„	Sinistral	Sinistral	
9.	„	Sinistral	Dextral	
10.	„	Sinistral	Sinistral	
11.	♀	——	Sinistral	
12.	„	——	Dextral	
13.	„	——	Dextral	
14.	♂	Dextral	Median	
15.	„	Dextral	Dextral	
16.	♂	Sinistral	Dextral	Faint roseate (Rose-white)
17.	♀	——	Dextral	Rose-white
18.	♂	Dextral	Dextral	Dark crimson
19.	„	Sinistral	....	White
20.	„	Sinistral	....	Light scarlet

Amphioxus is another example of a relatively fixed type which presents little range of variation, and less power of regeneration. Perhaps *Chiton* is another.

Sometimes the sheaths of the tentacles become perforated at some part of their length, and the tentacle may then issue from the adventitious orifice instead of from the apical orifice.

Not seldom among the shells of *N. pompilius* which are washed upon the reefs of New Guinea specimens are found in which the umbilicus is incompletely closed[1].

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[1] I have figured some examples of this umbilical aberration in *Quart. J. Micr. Sci.*, XXXIX., figures on Pl. 13, 1896, pp. 227—230.

Once a very abnormal shell was presented to me at Ralum in New Britain, in which the shell was divided into two nearly equal halves by a submedian raphe, reminding one of the shell-slit of *Pleurotomaria*. The raphe extended back over the involuted coils of the shell, and I am unable to decide whether it was due to an injury to the mantle or to some congenital malformation.

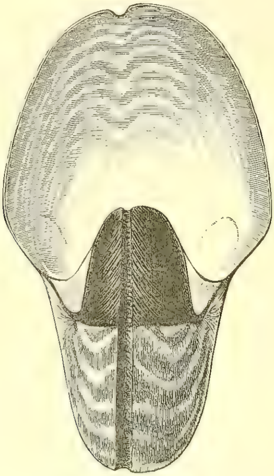


Fig. 15. Malformed shell of *N. pompilius*.

DESCRIPTION OF PLATES LXXV—LXXXIII.

PLATE LXXV.

Nautilus macromphalus, ♂. View of pallio-visceral region from below with the organs showing through by transparency.

Sketched from the fresh object, with natural colours, at Lifu, October 26th, 1896.

Each renal sac contains a bilobate renal follicle surrounded by the scarlet concretionary substance. The liver has a dark purple colour.

PLATE LXXVI.

FIG. 1. *N. pompilius*, ♀. Ventral view with reflected mantle, showing natural colours.

f.o. Funnel-organ.

a.i. *Ala infundibuli.*

x. Ligamentous limbus passing from funnel-organ over the surface of *s.m.* the shell-muscle.

m.e. Mantle-edge.

♀ Vulva.

br. 1 and *br.* 2. Branchiae.

osph. 1 and *osph.* 2. The osphradia.

nid. Nidamental gland.

v.p.o. Viscero-pericardial orifice.

b. Bristle passed into the opening of the duct of the pyriform gland.

a. Anus.

ac. Accessory nidamental gland.

The renal orifices occur (when the mantle is reflected) in front of the bases of the branchio-cardiac (efferent branchial) vessels.

FIG. 2. Renal concretions; the upper figure shows the concentric stratification under high magnification.

FIG. 3. *Harpa* sp. from Lifu seen from below to show the divisions of the foot, the semilunar *propodium* with sulcate border, the *mesopodium* and the *metapodium.* (Cf. text in explanation.) Natural size.

FIGG. 4 and 5. *Haliotis* sp. from New Britain. Anterior end of animal with shell removed, seen in ventral and dorsal view to illustrate the bilaminate, tentaculiferous *epipodium* (*ep.*) which is produced in front into a lobe which overlies the proboscis (buccal cone).

m. Mouth.

f. Platypodium (foot).

e. Eye-stalk.

Between the bases of the cephalic tentacles occurs a free flap of the integument resembling a nuchal membrane (Fig. 5). × 3.

N.B.—No portion of the mantle appears in either figure.

Fig. 6. *N. pompilius* juv. Dorsal view of a portion of the mantle-region of the same specimen as Pl. LXXVII. fig. 4.

d.p.i. The line of insertion of the dorsal lobe of the mantle into the body-wall.
s.m. Shell-muscle.
an. Annulus.
s.a. Septal aponeurosis.

The succeeding figures, unless otherwise stated, relate indifferently to N. pompilius and N. macromphalus.

Fig. 7. Piece of the posterior region of the mantle viewed from the inner or coelomic surface, to illustrate the connections of the siphuncle. The piece comprises the entire dorso-ventral extent of the insertion of the genito-intestinal ligament into the hinder wall of the perivisceral coelom.

g.l. Genito-intestinal ligament (cut across).
p.a. Posterior pallial artery.
p.v. Posterior pallial vein.
s.a. Siphuncular artery (sinistral).
r.s. Radical sinus of the siphuncle (pallio-siphonal sinus).
s. Siphuncle.

Fig. 8. Similar piece from another specimen. The posterior pallial vein and pallio-siphonal sinus have been laid open and a bristle passed into the siphuncular vein (axial cavity of siphuncle). The siphuncular artery (dextral) is seen in the floor of the pallio-siphonal sinus.

Fig. 9. Portion of a bisected shell of *N. pompilius* to illustrate the relation between the growth-lines of the shell (shell-lines), the concentric muscle-lines and the posterior border of the actual muscle-scar and annulus. An asterisk is placed opposite to the *linea limitans* of the muscular impression. The last-formed septum is thin and fragile, thickening not having yet taken place.

PLATE LXXVII.

Fig. 1. Frontal view of the fundus of the animal-chamber of a shell of *N. pompilius.*

1. Annular impression.
2. Septal suture or impression of the septal aponeurosis of the mantle.
3. Muscle-scar.
4. Border of the nacreous layer deposited by the dorsal lobe of the mantle over the black varnish which covers the normally banded periostracum of the anfractus of the shell.

Fig. 2. Specimen of female *N. macromphalus* with spermatophore (*sp.*) protruding from the oral sheath.

Fig. 3. *N. macromphalus* adhering to the substratum in a vertical position by means of its tentacles. More usually its position, when attached to any surface, is more or less horizontal, with the adhesive tentacles spreading about in all directions.

a.i. *Ala infundibuli* in diastole.

n.m. Nuchal membrane detached from the anfractus of the shell.

e. Eye with the ophthalmic tentacles on either side of it.

Fig. 4. Dorsal view of young *N. pompilius* to show relations of hood, nuchal membrane and mantle in the nuchal region.

n.m. Nuchal membrane passing round on either side to coalesce with the *alae infundibuli.*

b.w. Portion of body-wall between the base of the nuchal membrane and the line of insertion of the dorsal lobe of the mantle.

d.p.f. Dorsal lobe of mantle turned back.

s.m. Shell-muscle.

si. Siphuncle.

Fig. 5. Dorsal view of cephalic region of a male specimen of *N. macromphalus* in which the right anterior half of the hood had been apparently bitten away and the edges healed up.

f. Funnel.

m. Buccal cone.

sp. Cyst of spermatophore, with the apices of some of the extrabuccal tentacles exposed on either side.

s. Spadix.

Fig. 6. Similar view of another specimen in which a piece had been bitten out of the hood so as to expose the entire cyst of the spermatophore (*sp.*), which is held by the two dorsal tentacles of the extrabuccal series on each side.

PLATE LXXVIII.

Figg. 1 and 2. Two male *N. pompilius* from below with mantle drawn back, showing (in Fig. 2) *situs inversus* of the genital apparatus. These specimens are now in the Zoological Museum of the University of Cambridge.

v.n. Visceral nerves.

os′. Submedian osphradia, separated by an interval in Fig. 1, coalescent in Fig. 2.

n.s. Needhamian sac of the *vas deferens.*

Fig. 3. Side view of cephalopodial region of *N. umbilicatus* to show the character of the hood.

a. Sulcate tentacle of spadix (10th tentacle of the extrabuccal series).

b. Tessellate tentacle of spadix (11th of the series).

p.g. Preputial gland.

e. Root of eye, which had been removed by means unknown to me; a bristle is passed into the olfactory labyrinth.

f. Funnel

a.i. *Ala infundibuli.*

The digital tentacles of the left side have been cut away in order to expose the spadix.

Fig. 4. Cephalopodium of *N. macromphalus* with erected spadix. The hood has been divided in the middle line. Specimen deposited in the Museum at Cambridge.

g. Glans of spadix (9th tentacle of extrabuccal series).

sp. Cyst containing spermatophore.

c.e. Cut edge of hood.

e. Eye.

PLATE LXXIX.

FIG. 1. Portion of shell of *N. macromphalus* showing encrusting organisms in and near the umbilicus.

FIG. 2. Egg of *Nautilus macromphalus*, showing fenestrations and pectinations of the outer capsule. There is a deep median notch extending from the front end through about half the length of the capsule. × 1½.

FIG. 2 *a*. Portion of one of the pectinate ridges of preceding. These ridges seem to correspond with the annulations of the infrabuccal tentacles (cf. fig. 6 *a*).

FIG. 3. Same egg seen from the lower surface, showing the area of fixation.

FIG. 4. Secretory products of the nidamental gland. The oval bodies are formed in large bladder-like cysts. Zeiss 3 D, Cam. luc. Drawn from fresh object at Lifu, 9/2/97.

FIG. 5. Infrabuccal apparatus of immature female (*N. pompilius*).

FIG. 6. Infrabuccal apparatus of mature female (*N. pompilius*) with the subjacent portion of the cephalopodium.

o. Organ of Owen.
v. Organ of Valenciennes.
19. Nineteenth digital tentacle of the outer whorl.

FIG. 6 *a*. Enlarged drawing of one of the infrabuccal tentacles of preceding.

FIG. 6 *b*. Apex of one of the infrabuccal tentacles of same.

FIG. 7. Anterior portion of cephalopodium (*N. pompilius* ♀) with hood partially bisected and the flaps turned aside to show the inner whorl of tentacles embracing the buccal cone.

f. Funnel.
o. Organ of Valenciennes.
i.a. Infrabuccal apparatus.
e.l. Extrabuccal lobe.

FIG. 8. Buccal cone of female in side view, with buccal membrane pressed back to expose the jaws.

i.m. Lower jaw.
r. Teeth of radula.
s.m. Upper jaw.
i.a. Infrabuccal apparatus.
p. Marginal papillae of buccal membrane.

FIG. 9. Spadix of *N. macromphalus* (same as in Pl. LXXVIII. fig. 4) in frontal view.

g. Glans.
a. Sulcate tentacle.
b. Tessellate tentacle.
p.g. Preputial gland.

FIG. 9 *a*. Portion of sulcate tentacle enlarged, showing glandular pits.

FIG. 9 *b*. Similar portion of tessellate tentacle, showing glandular crypts.

FIG. 10. Same spadix from left side. The maximum length of this spadix is 65 mm.; the glans projects 28·5 mm. beyond its sheath; maximum width of glans, 25 mm.

FIG. 11. Infrabuccal apparatus of female (*N. macromphalus*) in state of erection. It seems likely that the tentacles of this organ take an active part in fashioning the outer capsule of the egg. (Cf. figg. 2 *a* and 6 *a* of this plate.)

FIG. 12. Infrabuccal organ (organ of Van der Hoeven) of the youngest male (*N. pompilius*) obtained. × 20.

FIG. 13. One of the outermost digital tentacles, to show the protuberant ridges towards the apex. × 2.

FIG. 14. Portion of an ophthalmic tentacle showing ciliated lamellae. (Reduced from figure published in *Quart. J. Micr. Sci.* 1897.)

PLATE LXXX. (*N. pompilius.*)

FIGG. 1 and 2. Views of the right (1) and left (2) extrabuccal series of tentacles in the youngest male obtained. The ventral group of four tentacles represents the spadix or the anti-spadix, but is, at this stage, exactly equal on both sides of the cephalopodium.

s. Cut edge of ventral symphysis.

FIG. 3. Young (sinistral) spadix showing unmodified apices of the tentacles protruding from their sheaths. × 3.

[The middle length of the hood of the original specimen was about 33 mm., and width, measured over the eyes, about the same.]

The letter *g* is placed upon the sheath of the first tentacle or *glans* of the spadix.

i. Cut edge of intercoronal membrane which was removed in order to expose the entire spadix which was sunk deeply behind it.

s. Cut edge of ventral symphysis.

FIG. 4. Outer aspect of same, showing *f.* the free tentacle of the spadix, partially concealed behind the membranous expansion of the sheath of the *glans.*

FIG. 5. The same, with sheaths of the tentacles laid open and the free tentacle (*f.*) cut off.

g. Glans.

FIG. 6. Another (dextral) spadix rather older than preceding, showing commencing reduction of the apical portion of the glans (*g.*).

f. Free tentacle of spadix.

FIGG. 7 and 8. Spadix (7) and anti-spadix (8) of an older specimen (middle length of hood nearly 40 mm., width across the eyes about 38 mm.). × 3.

The free tentacle of the spadix is, at this stage, the most prominent member of the series.

i. Cut edge of intercoronal membrane.

s. Cut edge of ventral symphysis, with the nineteenth digital tentacle of the outer whorl of the cephalopodium, beside it.

FIG. 9. Inner surface of the ventral symphysis of a young female (measuring 66 mm. from the root of the siphuncle to the anterior border of the hood), showing the commencing formation of the lamellae of the organ of Valenciennes. Natural size.

Fig. 10. The right extrabuccal lobe of the same specimen; free dorsal border on the left, cut edge below and on the right of the figure. The tentacles have attained their normal development (compare figg. 1 and 2). × 2.

FIG. 11. Infrabuccal apparatus of the same, presenting a prominent, transversely extended "organ of Owen" and lateral tentacles in a rudimentary condition. × 4.

FIG. 12. Portion of the inner surface of the ventral pallial fold of same, to show the primordia of the sheath of the nidamental gland; the lamellae of the gland (compare Pl. LXXVI. fig. 1) have not yet commenced to form. × 2.

o. Submedian osphradium.

FIG. 13. Infrabuccal organ of adult male from the ventral (aboral) aspect with the membranous sheath partially reflected to expose the lamellae (compare Pl. LXXIX. fig. 12). The total length of the organ was 26 mm. and the width 14 mm.

FIG. 14. Similar infrabuccal organ from another specimen viewed from the dorsal (adoral) aspect, with the wall cut away so as to expose the cavity of the gland and the glandular pits on the surface of the lamelligerous lobes (*l.*).

h. Cut edge of the fleshy wall of the gland; this wall is derived from, and adherent to the periphery of the lamelligerous lobes and peduncle of the organ, leaving only a narrow median passage (on the dorsal side) from the cavity of the gland to the exterior. In the dissection here figured the dorsal portion of the membranous sheath of the organ was divided by an incision passing through the median (dorsal) orifice.

FIG. 15. The same bisected so as to expose the inner or mesial surface of the left half of the gland, showing the free inner borders of the lamellae and of the lamelligerous lobe (*l.*).

p. Cut surface of the median portion or peduncle of the organ.

m^1 and m^2. Cut edges of the dorsal and ventral portions of the membranous sheath of the organ; the sheath is a derivative of the buccal membrane, i.e. the integument of the buccal cone.

FIG. 16. Male genital duct removed from the body.

b. *Ostium abdominale.*

gl. Glandular portion (phorogenic gland, containing a labyrinthine lumen in which the spermatophore is formed) of the *vesicula seminalis*, usually called the accessory gland.

a. Thin-walled antrum; in front of this region, the duct passes through the integument by a narrow neck and then dilates to form *n*, the Needhamian vesicle, which is connected with *p*, the penis or terminal portion of the duct, by a narrow sphincter.

Total length of *vesicula seminalis* (gland + antrum) 26 mm.

FIG. 17. Portion of the same with the antrum laid open showing the orifice perforating its floor by which the phorogenic gland communicates with it; a portion of a spermatophore is projecting freely through the orifice into the antrum. The roof of the antrum is perforated by another minute orifice with somewhat tumid lips, leading into the Needhamian vesicle.

Letters as in preceding figure.

FIG. 18. Another portion of the same. A piece of the wall of the Needhamian vesicle has been removed in order to expose the spermatophore which it contains and the saddle-shaped septum upon which the spermatophore rests.

Letters as in fig. 16.

FIG. 19. The spermatophore removed from the Needhamian vesicle, showing the notch occasioned by the septum of the vesicle.

FIG. 20. Pallio-visceral region of youngest male from below, chiefly to illustrate the

genital or, as called in the text, the genito-intestinal ligament, which represents a median mesentery. × 3.

t. Testis, derived from and adherent to the right side of the mesentery; on the opposite side is the gastric ligament passing across to be inserted into the wall of the stomach (*st.*).

p.a. Posterior pallial artery, seen traversing the middle pallio-visceral fontanelle (cf. Pl. LXXXII. fig. 7).

si. Siphuncle.

Figg. 21 and 22. Details of preceding, to elucidate the relations of the transverse and longitudinal loops of the intestine. Fig. 21 shows a portion of the intestine and right liver in normal juxtaposition. In fig. 22, the liver has been cut away so as to expose the intestine and the longitudinal loop of the latter has been turned forwards.

t.i. Transverse loop of the intestine.

d.i. and *a.i.* Descending and ascending limbs of the intestine.

oe. Narrow portion of the oesophagus proceeding from the fundus of the crop to the stomach (*st.*).

py. Pyloric caecum with bile-duct opening into its apex.

b.d. Bile-duct, above or behind which the intestine passes.

Fig. 23. Pallio-visceral region of another specimen older than that of fig. 20, but showing the same primary relations of the mesentery.

y. Pyriform gland.

st. Stomach traversed in this specimen by constrictions.

p.a. Posterior pallial artery.

d.i. and *a.i.* Intestine.

r.l. Right liver.

PLATE LXXXI.

Fig. 1. *N. pompilius.* Dissection of a relaxed specimen from the right side, showing the relation of the capito-pedal cartilage to the siphonopodium and to the cephalopodium. The *alae infundibuli* have been cut away.

f. Funnel (*crura infundibuli*).

l. *Limbus.*

c. Cartilage.

v. Infundibular vein.

a. Infundibular artery.

r. Rhinophore.

o.a. and *o.p.* Anterior and posterior ophthalmic tentacles.

e. Eye.

1—11. sheaths of digital tentacles; that of the second tentacle (2) comprises an anterior portion forming part of the hood and a posterior portion; the third sheath (3) is wedged in between 2 and 4, only its anterior end being visible in this view.

Fig. 2. Diagram of *Nautilus* to illustrate the theory of orientation. The dotted line denotes the presumptive antero-posterior axis.

l. *Limbus.*

a.i. *Ala infundibuli.*

s.m. Shell-muscle.

m. Mantle.

s.a. Septal aponeurosis.

Figg. 3 and 4. Diagrammatic sections through the cephalopodium of female (3) and male (4) to elucidate the tentacular formula suggested in the text. The ophthalmic tentacles are not included in the diagrams. On the left of fig. 4 there is the scheme of enumeration of the digital tentacles of the outer whorl, the tentacles being here regarded as marginal appendages of a sinuous pleural fold or epipodium.

c.p. Marginal papillae of the mouth.
m.i. Inferior mandible.
s.s. Superior symphysis of the cephalopodium.
i.s. Inferior symphysis.
f. Funnel.
ext.t. Outer whorl of the cephalopodium.
int.t. + *inf.o.* Inner whorl.
inf.o. Infrabuccal organ.

Fig. 5. *N. pompilius* ♂. Dissection from below to illustrate, among other points, the ventral symphysis of the cephalopodium which presents a deep concavity, *f.i.* the *fossa infundibularis,* to receive the funnel. The numbers are placed upon the sheaths of the tentacles involved in this view, in accordance with the scheme of enumeration here adopted. The funnel has been sliced away to its roots and the *vena cava* and endochondral sinus laid open to expose the fenestrations in their dorsal wall.

r.i. *Radix infundibuli.*
c.i. Cartilage.
a.i. *Ala infundibuli.*
v.i. *Vena cava.*
s.m. Shell-muscle (cut across).
n.s. Needhamian vesicle.
e. Eye.

Fig. 6. *N. pompilius.* Dissection of the cephalic sensory complex from the right side, showing also the origin in sequence from the coronal (pleuro-pedal) ganglion, of the nerves of the sixth, seventh and eighth digital tentacles.

a. Infundibular artery traversing the cartilage.
a.i. Cut surface of *ala infundibuli.*
c. Cartilage.
c.v. Cerebro-visceral nerve-centre.
h. Cut surface of hood.
l. *Limbus infundibuli.*
n. Olfactory labyrinth (rhinophore) laid open.
n.m. Nuchal membrane.
n.n. Olfactory nerve.
o.p. Posterior ophthalmic tentacle.
op.n. Optic nerves.
ot. Otocyst, lying over against the coronal ganglion, concealing the mass of the latter (cf. Pl. LXXXII. fig. 6).
s.m. Surface of shell-muscle.
v. Infundibular vein.

Fig. 7. *N. pompilius.* Dissection of the nuchal complex from above. The hood and nuchal membrane have been divided along the mid-dorsal line and the halves drawn apart,

exposing the peristomial and peri-oesophageal haemocoels and the diaphragm which separates them from one another behind the cerebral capsule.

a.i. Dorso-posterior portion of *ala infundibuli.*

ao.s. *Aorta superior.*

a.p.a. Anterior proventricular artery.

b.c. Buccal cone.

c.c. Cerebral capsule attached to neighbouring structures by conjunctive trabeculae and produced in front as a broad lobe.

cr. Crop.

m.i. Inferior mandible.

n.m. Nuchal membrane.

pr.m. Protractor muscle of the buccal cone.

r.i.m. and *r.s.m.* The dorsal retractor muscles of the buccal cone, *r.i.m.* attached to the inferior, *r.s.m.* to the superior mandible.

N.B. The cerebral commissure only occupies the posterior band-like portion of the massive fibrous capsule. It is possible that this fibrous capsule represents a primordial condition of the cartilaginous capsule of Dibranchs which is not, I think, homologous with the capito-pedal cartilage of *Nautilus*, the latter being essentially a funnel (siphonal) cartilage and not a cranial cartilage.

PLATE LXXXII.

FIG. 1. *N. macromphalus* ♂ juv. Innervation of the infrabuccal organ (organ of Van der Hoeven). The nerve to each lamelligerous lobe (i.e. to each half of the organ) ends abruptly, giving off the lamellar nerves as shown on the right side only (left of the figure).

m. Shallow secondary fold of the buccal membrane which would form the adoral portion of the sheath of the organ.

The middle length of the hood of the specimen was 52 mm.; the longer diameter of each lobe of the infrabuccal organ measured 5 mm.

FIG. 2. *N. pompilius* ♂ juv. Innervation of infrabuccal organ ascertained from an injected specimen.

a, *b* and *c*. Branches of the infrabuccal artery which accompanies the nerve.

Middle length of hood 65·5 mm.; length of infrabuccal organ 6 mm.

FIG. 3. Topography of the infrabuccal organ of the male. The fore-part of the funnel has been cut away and the ventral symphysis divided down the middle, thus exposing the ventral portion of the peristomial haemocoel, the organs which project into it and the nerves and vessels which traverse it. The dotted line represents the limit of the fundus of the external *fossa buccalis.*

p.c. Capsule of the coronal (pleuro-pedal) commissure, from which a small median artery issues and, passing freely across the haemocoel, enters the fundus of the infrabuccal organ.

n. Infrabuccal nerve accompanied by the artery.

l.i. *M. levator infundibuli.*

c.i. Cartilage.

a.i. *Ala infundibuli.*

FIG. 4. Somewhat similar dissection of female (*N. macromphalus*). The fundus of the peristomial haemocoel is exposed from the ventral aspect.

i.o. Infrabuccal organ (only the sheaths of the tentacles indicated on either side of the organ of Owen).

e.b. Extrabuccal lobe.

c.e. Cut edge of buccal membrane.

i.n. Infrabuccal nerve.

n.f. Infundibular nerve.

p.c. Coronal (pleuro-pedal) commissure.

a.c. *Arcus cartilaginis.*

i.r. Ventral retractor muscle.

N.B. The actual distance between the roots of the infundibular nerves was 14 mm.; between the infundibular and infrabuccal nerves on each side, 4 mm.

FIG. 5. Another dissection (*N. pompilius* ♂) exposing the fundus of the peristomial haemocoel; the funnel and oral sheath (cephalopodium) have been sliced away and the buccal cone turned back.

Letters, commencing from left side of figure:—

r.a. Recurrent tentacular artery.

o.s. Orifice of ophthalmic sinus.

c.s. Orifice of spadical sinus (a spacious reservoir surrounding the base of the spadix, probably assisting, by blood-pressure, in the protrusion of the latter).

i.n. Infrabuccal nerve.

n.i. Infundibular nerve.

a.i. *Arcus cartilaginis.*

c.c. Coronal commissure.

i.r. Ventral retractor.

c.i. Cartilage.

l.i. *Levator infundibuli.*

e. Eye.

h. Hood.

Between *a.c.* and *c.c.* lies the passage leading from the peristomial haemocoel into the endochondral sinus.

FIG. 6. Dissection resembling that of Pl. LXXXI. fig. 6, but carried further. The ophthalmic sinus is cut open, the rhinophore pulled aside, and the otocyst turned back.

a.o.t. Anterior ophthalmic tentacle.

a.o.n. Anterior ophthalmic nerve.

I. Hood-nerve.

II.—VIII. Digital nerves. (Between II. and V. occurs the common root of III. and IV.)

v. Visceral nerve-collar cut across.

o. Otocyst, turned back to expose the massive coronal ganglion.

o.g. Optic nerve-ganglion complex.

p.o.n. Posterior ophthalmic nerve, taking a recurrent course in the wall of the ophthalmic sinus, mediad of the optic ganglion (the posterior ophthalmic tentacle itself is quite concealed behind the eye in this view except for the apex which happens to project forwards between the eye and the hood).

r. Rhinophore.

e. Eye.

Fig. 7. Dissection of the pericardium from below to show the three fontanelles in the pallio-visceral ligament leading from the pericardium to the perivisceral coelom. [Reduced from *Quart. J. Micr. Sc.*, Vol. xl. 1897, Pl. II. fig. 2.]

p.l. Pericardial ligaments.
p.g. Pericardial glands.
b.c. Branchio-cardiac vessels.
a.p.a. Anterior pallial artery.
py. Pyriform gland.
g.d. Genital duct.
r.s. Outer renal sac (cf. Pl. LXXV.).

The pyriform body and its ligament form part of the outer border of the middle fontanelle and here somewhat encroach upon it so as to disguise its full extent. The posterior pallial artery is seen crossing the ventral surface of the heart, disappearing behind the pyriform ligament through the middle fontanelle. The heart is bound to the pallio-visceral ligament (which constitutes the fundus of the pericardium) by the cardiac ligament.

Fig. 8. Dissection of the branchial apparatus of the right side. The membranous portion of the mantle has been turned back and partly removed. The efferent trunk ($b.c.^2$) of the larger gill has been cut across and the gill itself turned partly round to present the afferent surface which has been laid open to expose the cavity of the reno-branchial vessel ($r.b.^2$). The portion of the latter which lies within the pericardium is left intact.

c.e. Cut edge of the mantle at the junction of its membranous and visceral portions.
r.s. and *p.g.* Renal sac and pericardial gland of the macrobranchiate segment.
$b.c.^2$ Extra-pericardial and intra-pericardial portions of the branchio-cardiac trunk.
$b.c.^1$ Branchio-cardiac vessel of the lesser gill (seen lying across in front of the greater gill).
v. Heart.
p.v.l. Pallio-visceral ligament.
p.l. Pericardial ligaments.
a. Position of annulus.
s. Position of septal aponeurosis.
m. Mantle.

Fig. 9. Portion of body behind the funnel to show veins entering the *vena cava.*

f.o. Funnel-organ.
l. *Limbus* or ligament passing from *f.o.* over the surface of the shell-muscles.

Fig. 10. Ventral view of the pallio-visceral region of *N. pompilius*, to show the paired pallial veins as displayed by automatic injection with air or gas after removal of the animal from the shell. The finest ramifications of the veins throughout the substance of the membranous portion of the mantle are thus revealed, but only the main branches are shown in the drawing.

PLATE LXXXIII.

Figg. 1 and 1 *a*. Amoebocytes (blood-corpuscles) of *N. macromphalus.* They undergo relatively rapid amoeboid changes of form; some contain fine granules, but most of them are laden with coarse, bluish, refringent granules which dissolve away in acetic acid leaving a spongy plasmatic reticulum. The cells vary in size and tend to accumulate in masses on the slide, sometimes appearing to form plasmodia (fig. 1 *a*). When killed and stained with acetic acid and alum cochineal the nucleus presents a chromatic reticulum. Zeiss Oc. 3, Obj. J, water imm., Cam. luc.

FIG. 2. Otocones. Zeiss 3 J, Cam. luc.

FIG. 3. Sagittal section (parallel to long axis of body) through one of the submedian osphradia. Only the epidermis and nerves are drawn. The limits of the sensory epithelium are indicated by slight elevations near the borders of the figure. A large nerve proceeding through the conjunctive framework from below is seen to branch and then penetrate through the basement-membrane into the substance of the epidermis, where it terminates in an intra-epidermal fibrillar plexus. Zeiss 3 A.

b.m. Basement-membrane.

n. Nerves with subcutaneous and intra-epidermal course.

FIG. 4. Portion of a similar section more highly magnified, showing a remarkable intra-epidermal fibrillar plexus. Zeiss 3 D; Cam. luc.

FIG. 5. Tangential section through the epidermis of a submedian osphradium taken through one of the angles made by the papilliform lobes (which arch over and protect the sensory surface of each submedian osphradium) with the base of the osphradial groove. The ramifying intra-epidermal fibrillar plexus is well shown, and there are also indications of the occurrence of peripheral ganglion-cells. Zeiss 3 C, Cam. luc.

FIG. 6. Papilla of an interbranchial osphradium showing cilia. Drawn from the living object and reproduced from *Quart. J. Micr. Sc.*, 1897.

FIG. 7. Section through an interbranchial osphradium cutting the papilla lengthwise, i.e. at right angles to the long axis of the body, showing the papilla itself and the subjacent surface of the mantle. The sensory surface occupies a well-defined tract about the angle made by the papilla with the mantle. Cilia not shown in the drawing.

o.p. Apex of the osphradial papilla.

n. Subcutaneous and intra-epidermal nerves.

FIG. 8. Enlarged view of the intra-epidermal termination of a nerve (*n.*) in an interbranchial osphradium.

FIG. 9. Transverse section through the siphuncle showing the central sinus (siphuncular vein) and peripheral lacunae communicating with it.

a. Main artery of the siphuncle.

d. and *v.* Dorsal and ventral surfaces of the siphuncle.

FIG. 10. Portion of the wall of the siphuncle showing the intra-epidermal prolongations of the subcutaneous lacunae. Zeiss 2 D, Cam. luc.

s. Subcutaneous blood-spaces or lacunae.

t. Trabeculae.

FIG. 11. Longitudinal section through siphuncle, showing the axial vein communicating with the peripheral lacunae.

s. Axial sinus or vein; (the index lines pointing to the sides of the sinus should not have been inserted).

FIG. 12. Portion of wall of preceding, showing the longitudinal course of one of the intra-epidermal blood-channels.

s. Venous space.

FIG. 13. *Rete mirabile* seen through the epidermis of the funnel-organ in the fresh state.

FIG. 14. Portion of endochondral sinus showing a valve arching over the capito-pedal orifice. An arrow is passed from the tubular sinus in which the levator muscle of the funnel lies, into the endochondral sinus.

c. Cartilage.
v. Valve.

FIG. 15. Ovarian ovum of an injected specimen, removed from the body and viewed from the animal pole showing the ramifications of the genital artery in the follicle.

FIG. 16. Enlarged view of portion of preceding.

FIG. 17. Section through an ovarian ovum, showing the intra-lecithal processes of the follicle.

FIG. 18. Abnormal egg of *N. macromphalus*, with defective capsule exposing the vitellus at three places. The outer capsule was only present on one side of the egg, namely, on the side opposite to that figured.

FIG. 19. Inner capsule of an egg of *N. pompilius* from below, showing clear mesial longitudinal tract separating the striations of the remaining surface. The outer capsule has been removed except in the region of its median and lateral attachments to the inner capsule.

FIG. 20. Pear-shaped inner capsule of egg of *N. macromphalus* from below. The outer capsule has been removed except at the hinder end in the region of the irregular disc of attachment which presents a spongy cavernous surface. The striations of the inner capsule tend to run longitudinally below and transversely on the upper side of the egg.

FIG. 21. Egg of *N. macromphalus* from above, with the longitudinal slit in the upper wall of the outer capsule widened out so as to expose the inner capsule with its striated surface. Reproduced from *P. R. Soc. London*, Vol. LX. 1897, p. 470, fig. 4.

FIG. 22. *N. macromphalus.* Inner capsule of egg seen from below (i.e. from the side directed towards the disc of attachment). Half the lower wall of the capsule has been removed by slitting along one of the lateral sutures and along the median groove (depressed longitudinal tract) to show the brown-coloured vitellus lying in the capsule. The lateral sutures are continued into each other at the front of the capsule so that the inner capsule is really bivalvate. The germinal disc (not indicated) occurs at the anterior pole of the vitellus, the orientation of the laid egg coinciding with that of the ovarian egg (cf. text-fig. 13).

FIG. 23. *N. macromphalus.* Inner capsule of egg in side view, showing the dorsal ridge with its anterior terminal process and the lateral suture. A fragment of the outer capsule remains at the hinder end, the rest having been cut away.

FIG. 24. Enlarged view of one of the nascent tentacles of the extrabuccal series shown in Pl. LXXX. figg. 1 and 2.

The tentacle appears as a minute papilla and the sheath seems to grow round it as a dermal fold with a simple border in front and a deep notch (possibly indicating concrescence of the two halves of the fold) at the back of the tentacle. Zeiss 3 A.

FIG. 25. Macroscopic view of the eye in vertical section. The plane of section lies on one side of the pinhole aperture so that this is seen intact from the interior of the optic cup. The bacillary layer representing the vitreous body forms a thin sheet over the

black retina except over the inner surface of the opaque cornea which appears as a black disc perforated by the pinhole orifice.

The dorsal border of the eye is smooth and convex, the ventral border limbate. × 3.

r. Rhinophore.

Fig. 26. View of the anterior portion of the peri-oesophageal haemocoel. The body has been divided in the nuchal region. The visceral nerves are seen radiating out from the visceral ganglionic commissure.

d. Diaphragm (the darkly shaded area in front of and above the bifurcating aorta) separating the peristomial haemocoel from the peri-oesophageal haemocoel.

a. Aorta.

n.m. Nuchal membrane.

h. Hood.

oe. Oesophagus.

s.m. Shell-muscle.

v.c. *Vena cava.*

f.o. Funnel-organ.

a.i. *Ala infundibuli.*

Fig. 27. The funnel with the flaps pressed open to expose its internal surface. The regions of the *crura* and *alae* are separated by the anterior borders of the cartilage appearing as oblique, whitish bands. Between the *crura* occurs the tongue-shaped valve, the free border of which is approximately concentric with the anterior border of the funnel.

f.o. Funnel-organ.

Fig. 28. Dissection of an injected specimen to exhibit the recurrent course of the tentacular artery. (Cf. also Pl. LXXXII., fig. 5.)

a. Aorta.

r.m. Roots of dorsal retractor muscles.

c.e. Cerebral ganglionic commissure cut across; the roots of the two stomatogastric nerves of the right side are seen beyond the cut edge, but the demarcation of the cerebral commissure could not be well indicated in this drawing.

g. Coronal (pleuro-pedal) ganglion.

r.a. Recurrent tentacular artery.

Fig. 29. Dissection of the buccal cone from the right side, to illustrate the topography of the stomatogastric system.

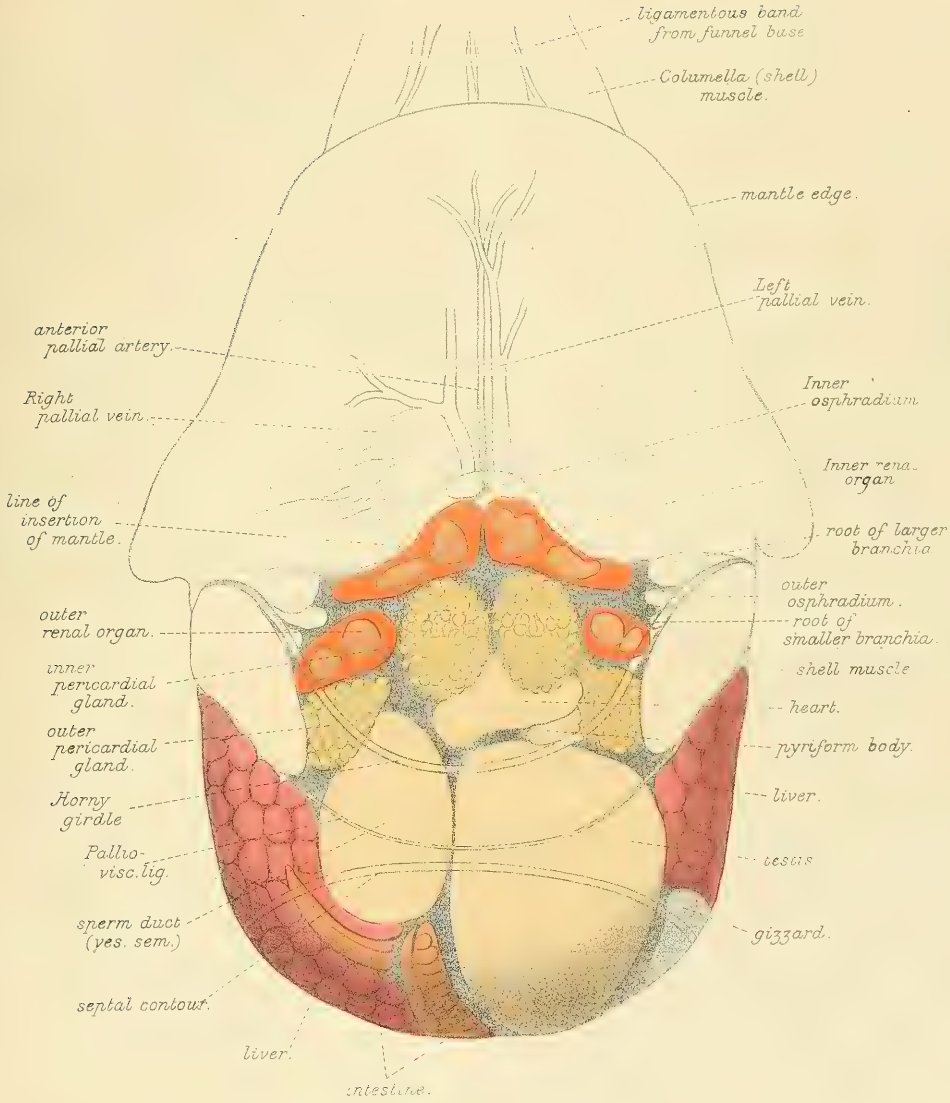
r.m. Retractor muscle.

a. Buccal artery.

r. Radular caecum.

n^1. and n^2. Stomatogastric nerves meeting in the pharyngeal ganglion below the border of the wing-like expansion of the lower mandible (n^2. is cut across shortly before the union).

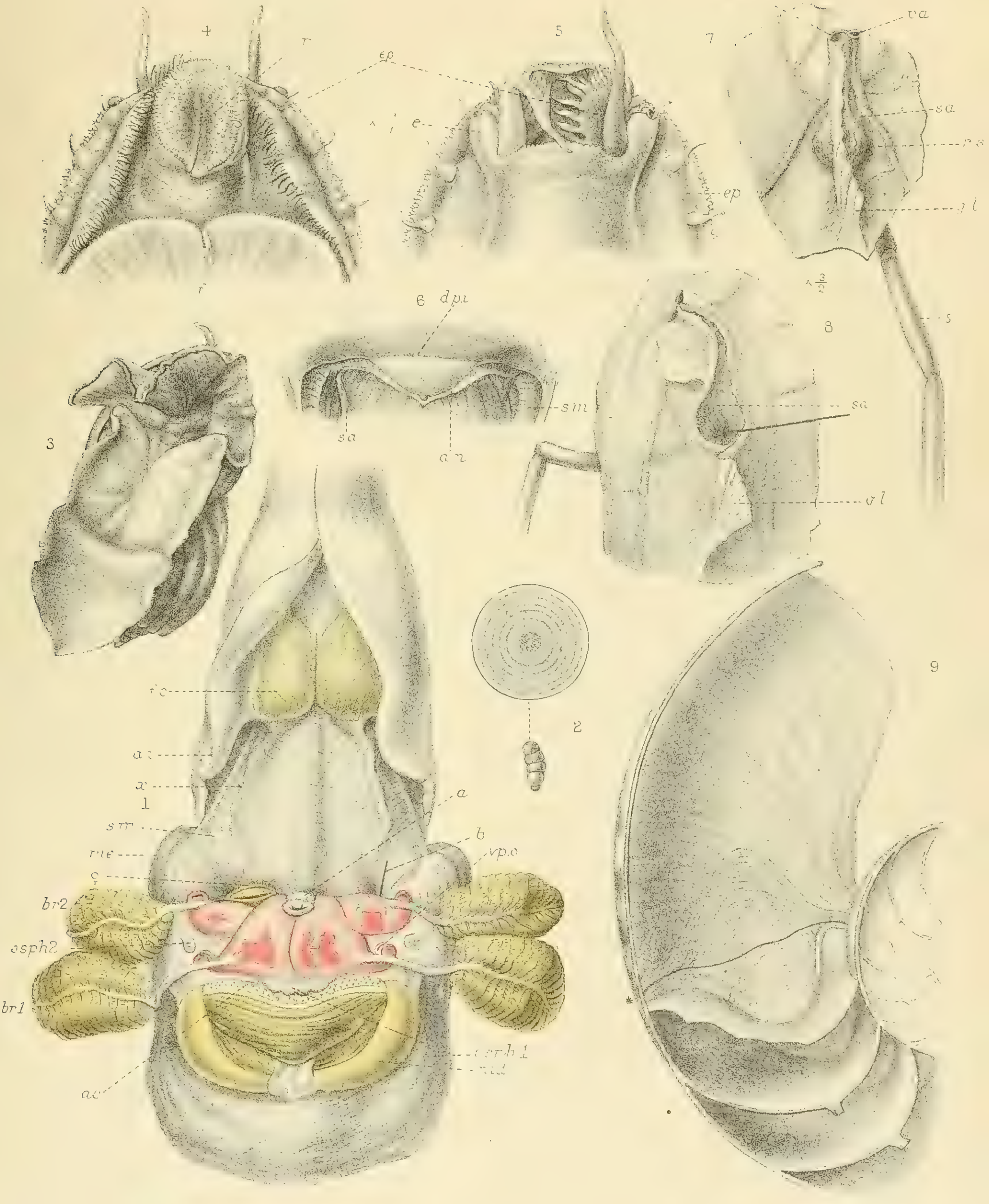
$b.c.^1$ and $b.c.^2$ Buccal commissures proceeding from the pharyngeal ganglion.



A. Willey del. ad nat.

West, Newman chromo.

NAUTILUS MACROMPHALUS ♂



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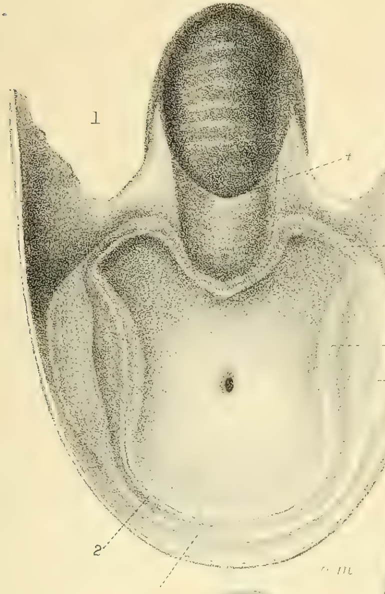

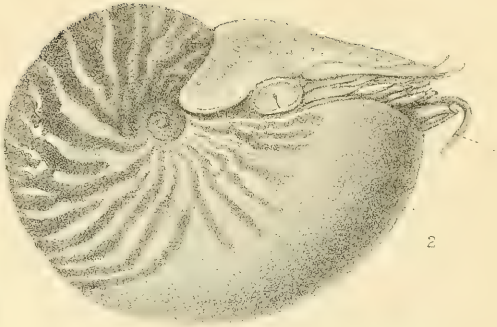

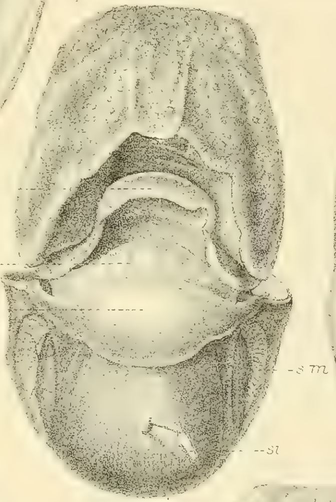

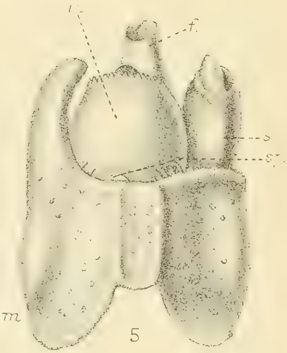

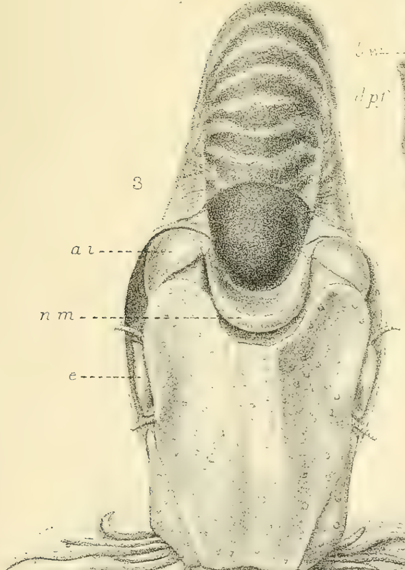

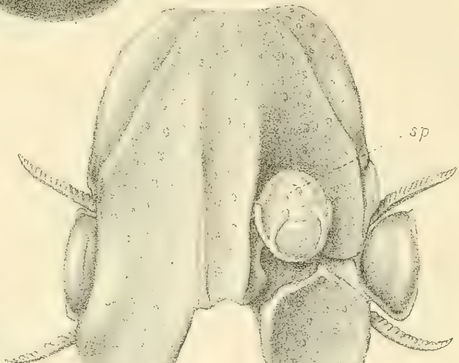

P. Highley & A. Willey del. West, Newman lith

NAUTILUS

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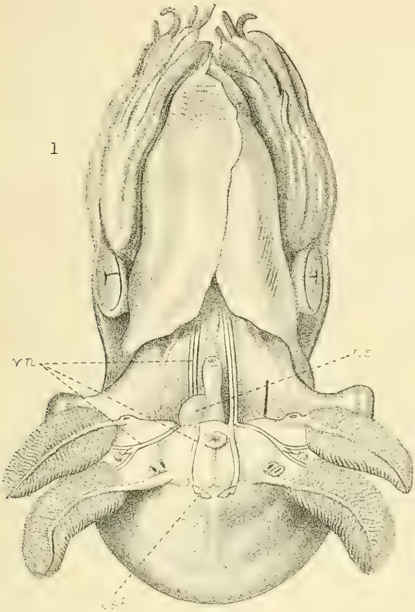

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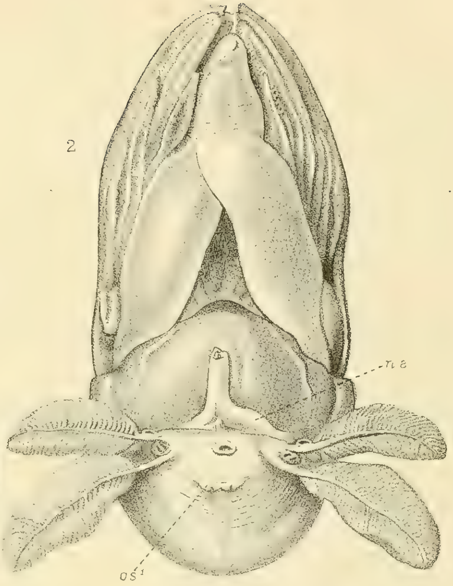

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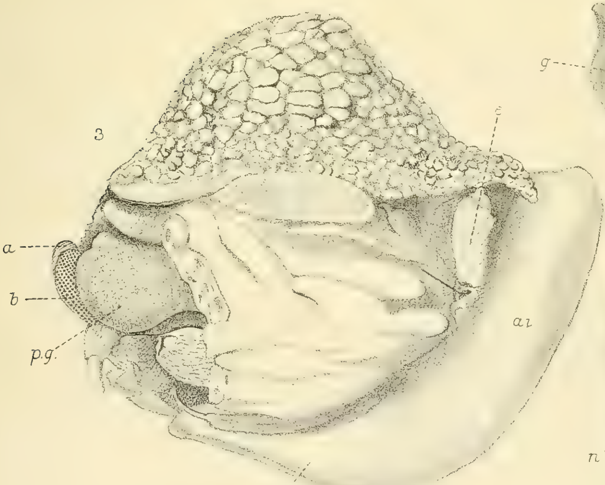

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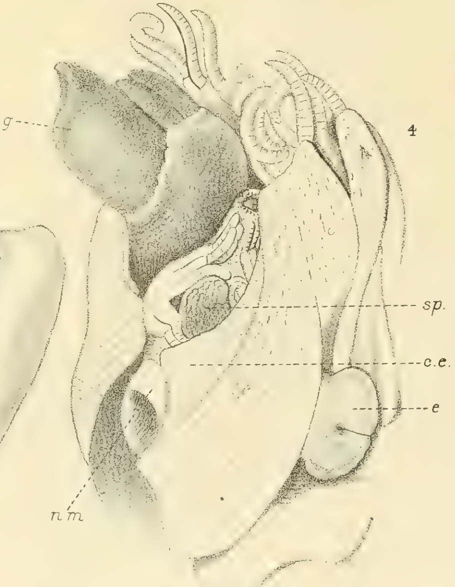
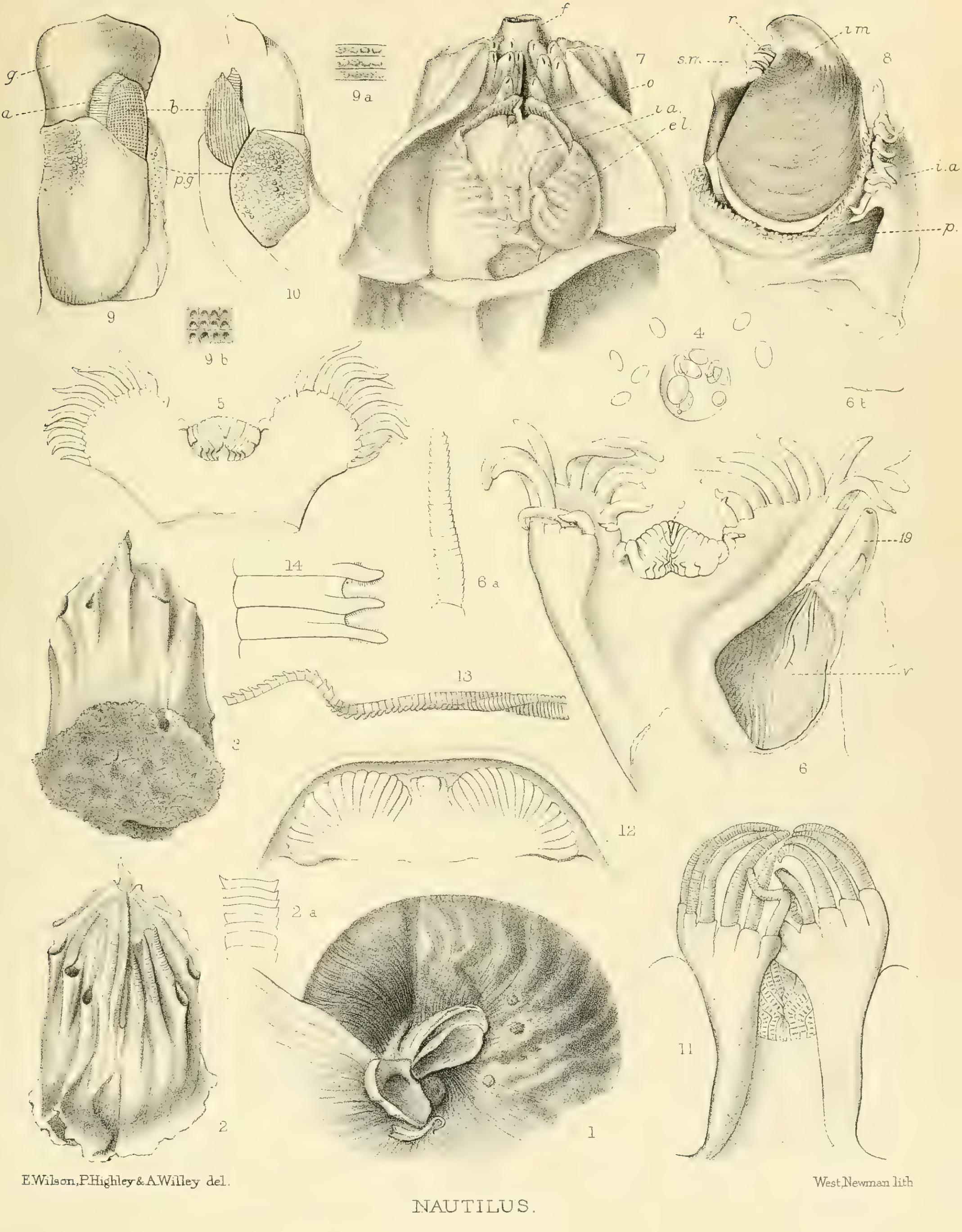


Edwin Wilson del.

West, Newman lith.

NAUTILUS.



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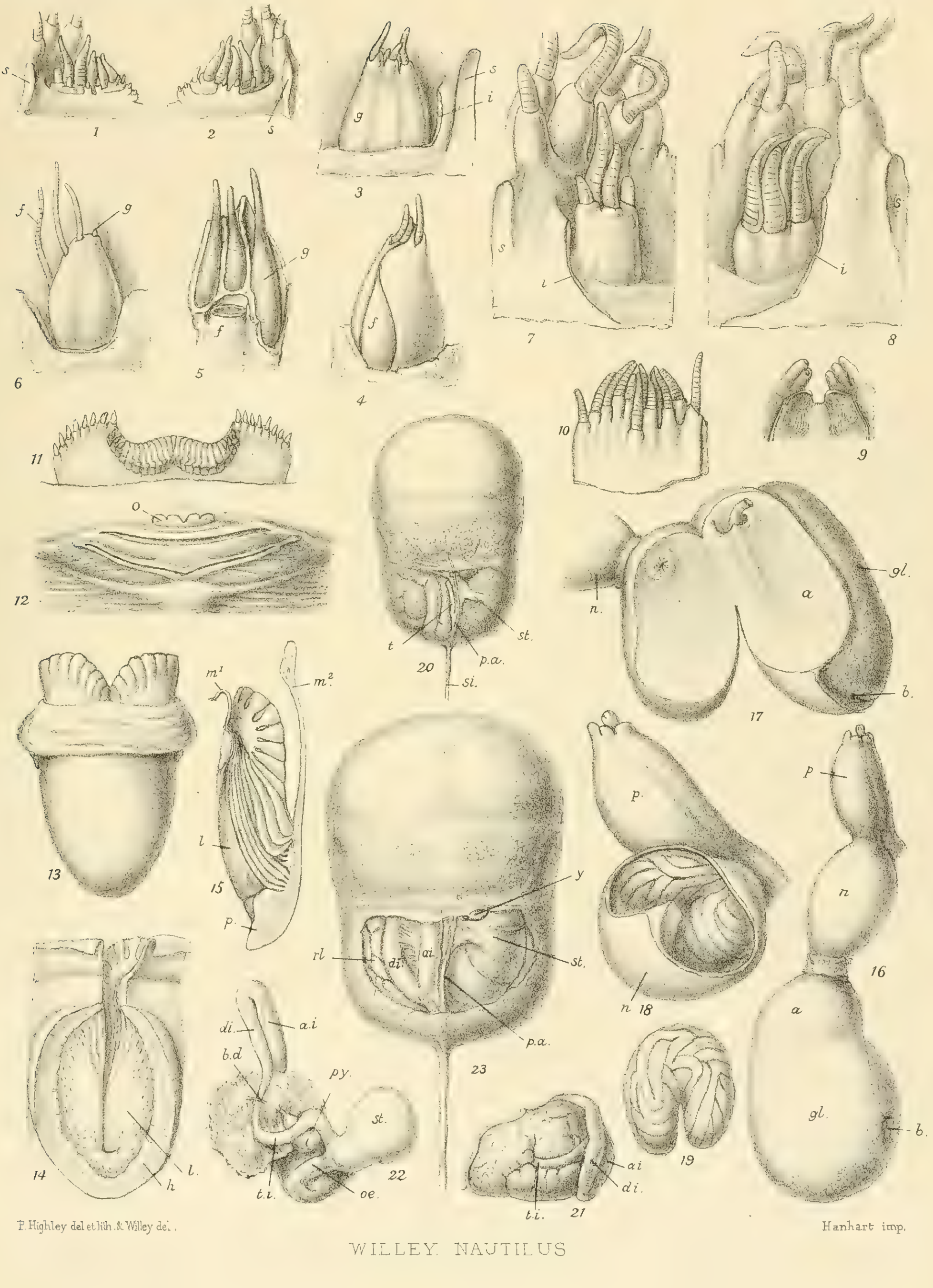

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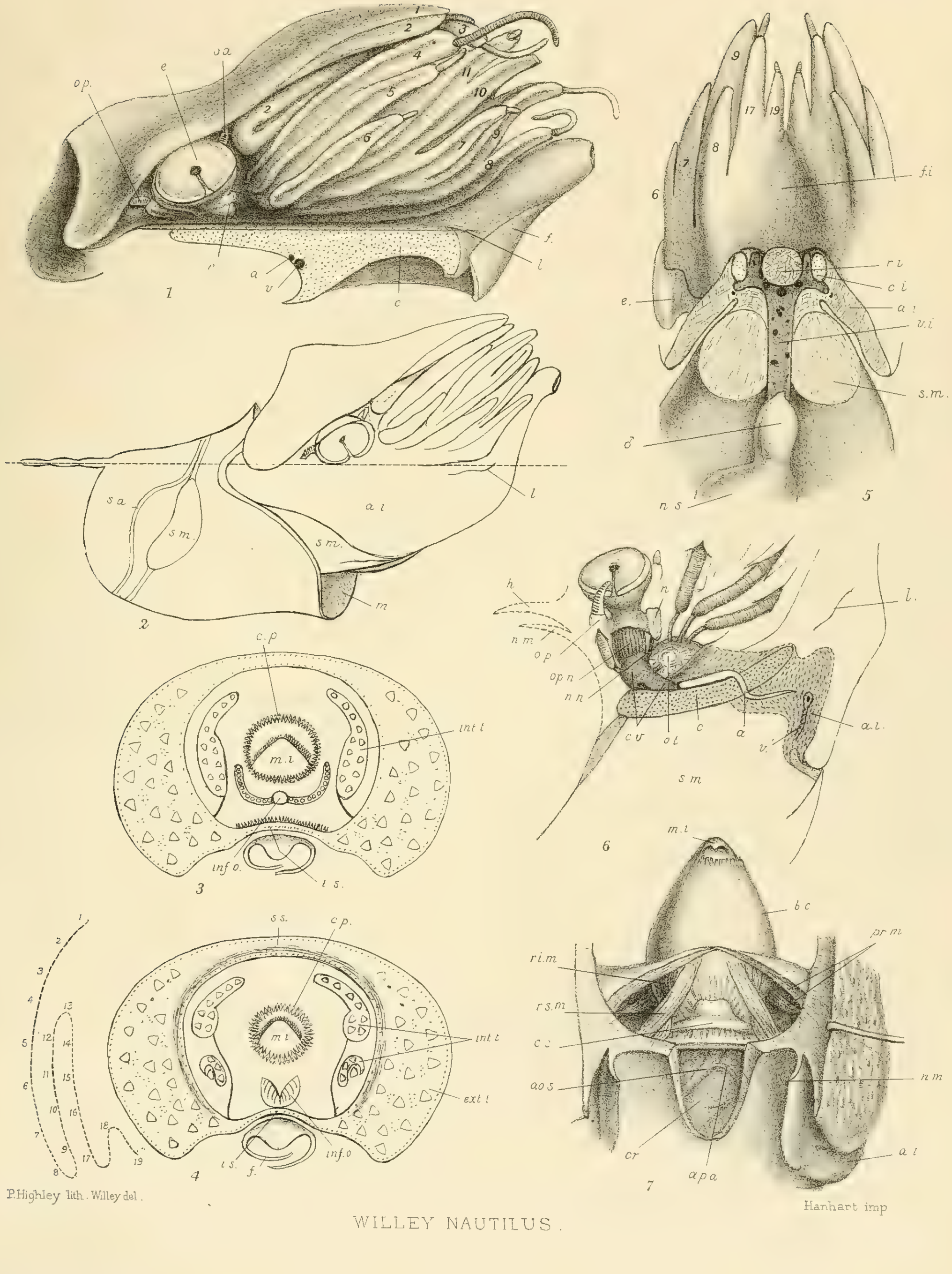

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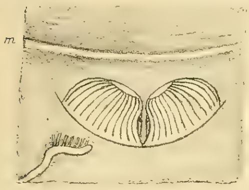

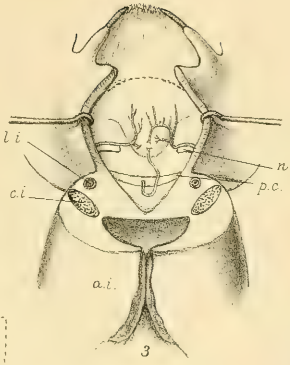

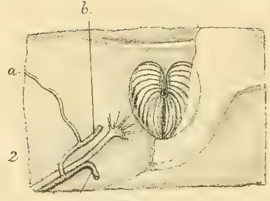

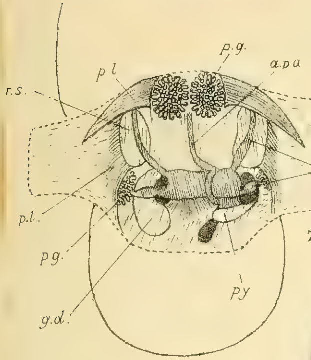

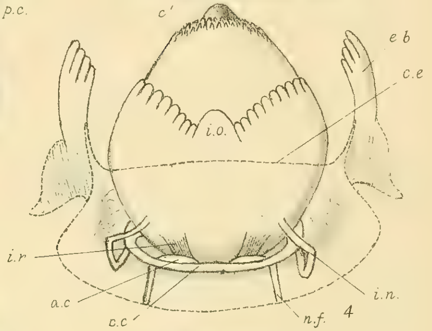

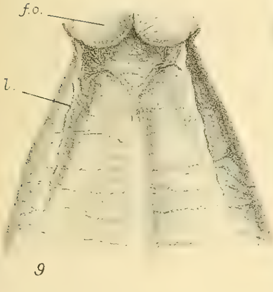

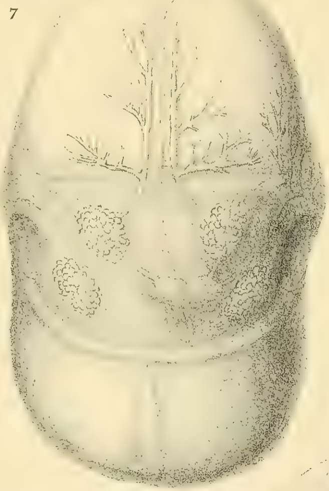

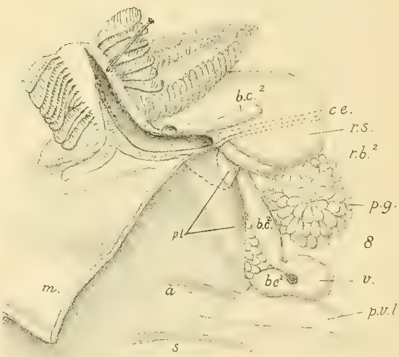

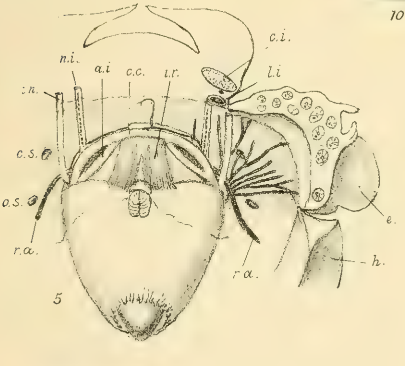

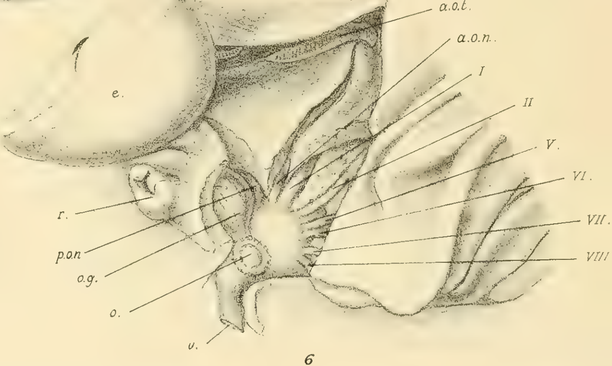

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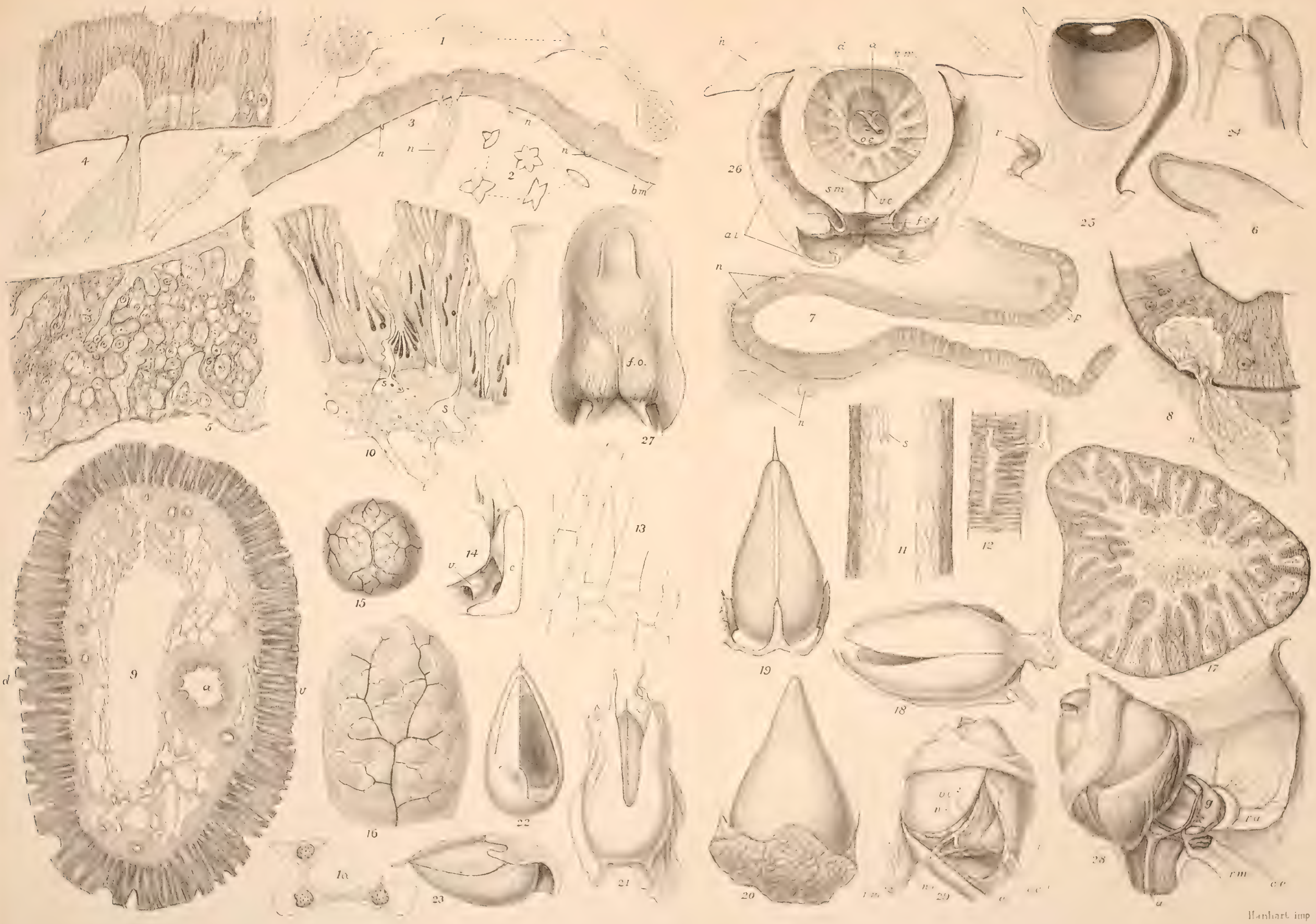

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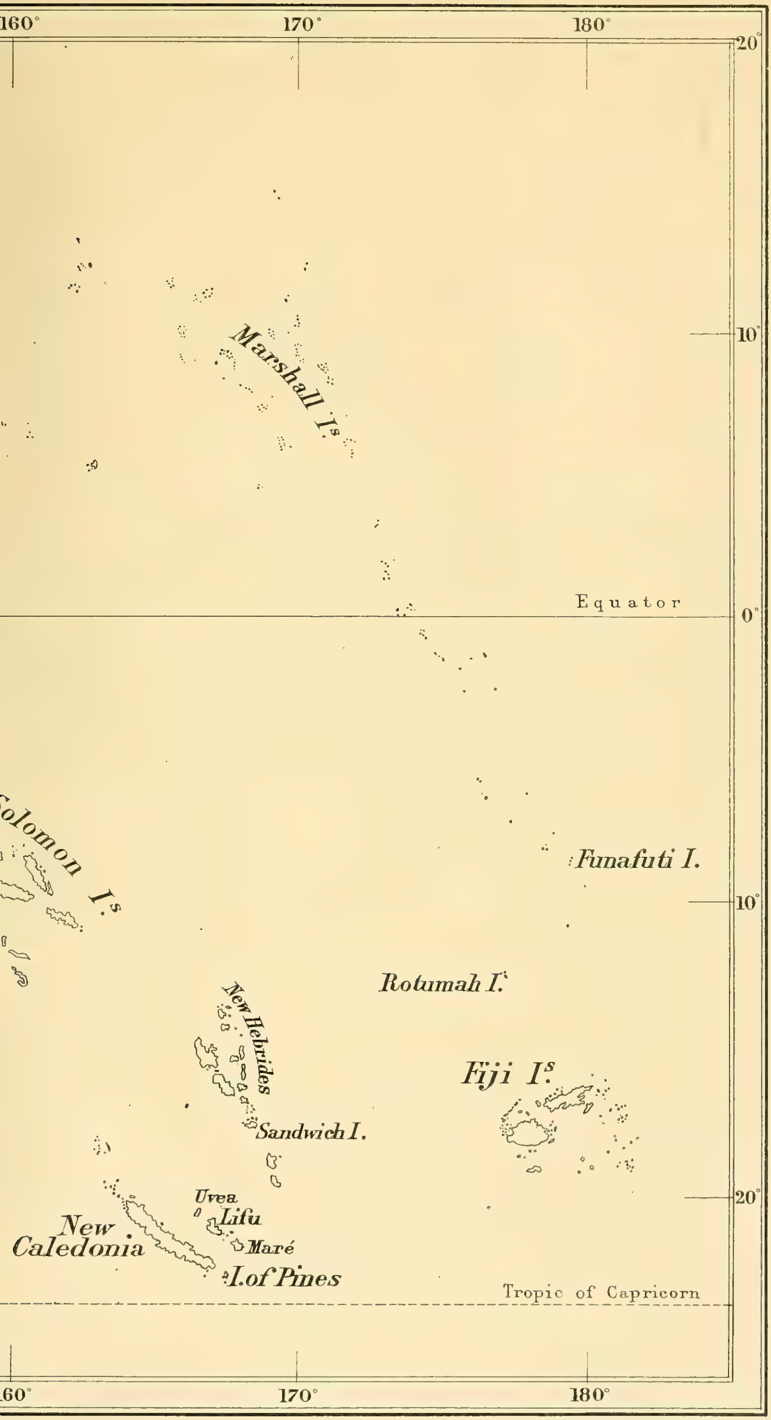

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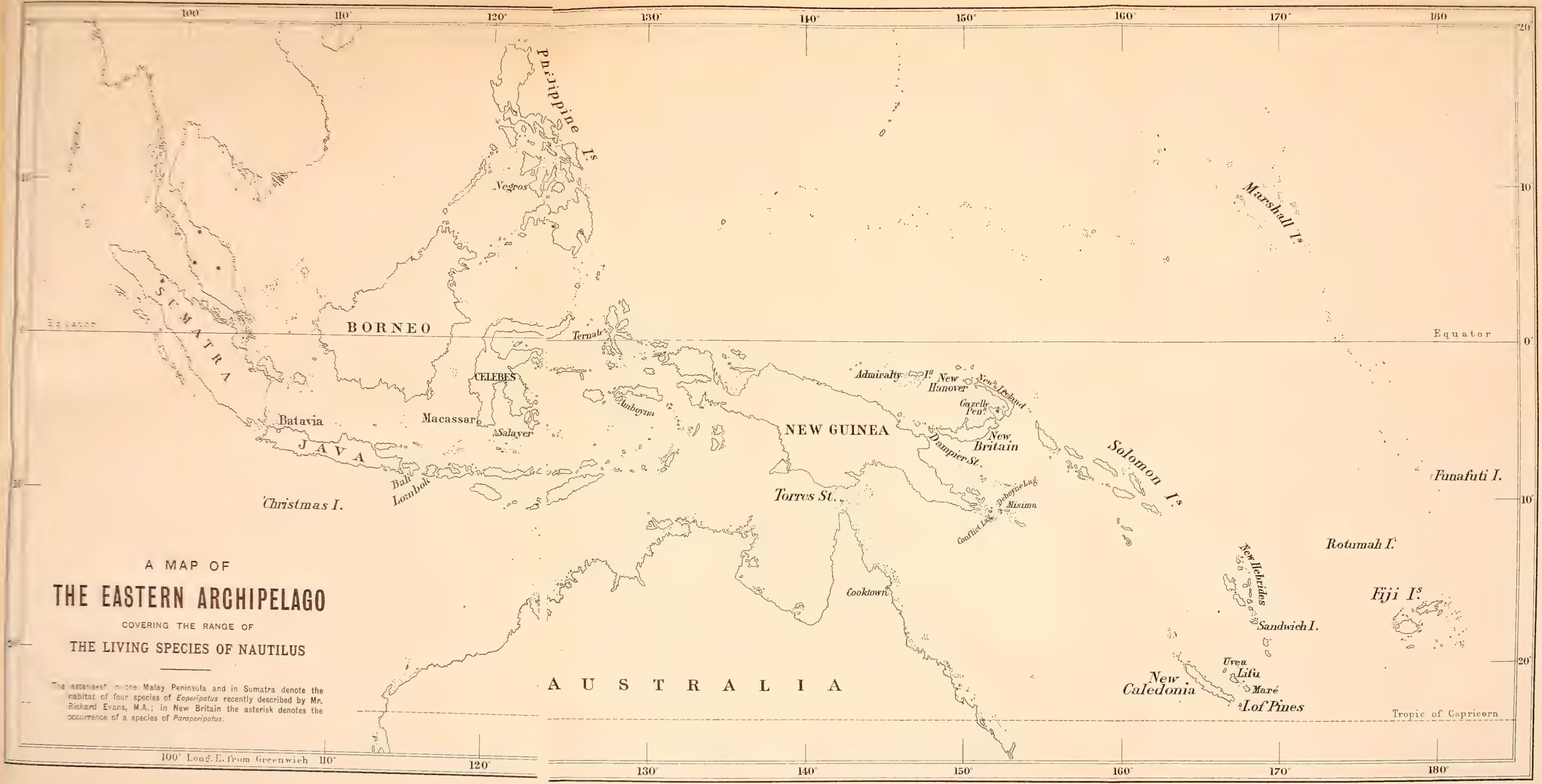

A MAP OF

THE EASTERN ARCHIPELAGO

COVERING THE RANGE OF

THE LIVING SPECIES OF NAUTILUS

The asterisks* in the Malay Peninsula and in Sumatra denote the habitat of four species of *Eoperipatus* recently described by Mr. Richard Evans, M.A.; in New Britain the asterisk denotes the occurrence of a species of *Paraperipatus*.

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